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THE ECOLOGY OF TROUT STREAMS IN YELLOWSTONE NATIONAL PARK

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INTRODUCTION

Under the auspices of the Roosevelt Wild Life Forest Experiment Station at the New York State College of Forestry, Syracuse, N. Y., the writer was afforded an opportunity during the summer of 1921 to examine and study trout streams in the northwestern section of Yellowstone National Park. Camp Roosevelt, operated by the Yellowstone Park Camps Company, was the base from which these studies were made, covering the period from June 18 to September 9, inclusive.

Due to unforeseen complications, chiefly in the way of health and change of position, the completion of the manuscript was delayed till 1927. In the meantime the writer has had ample opportunity to study other mountain streams in a comparative way in Idaho, Washington and Montana. Chief among these are the Palouse, Clearwater, Oro Grande, Snake, and St. Joe rivers in Idaho and Washington; and the streams comprising the MacDonald drainage, Two Medicine drainage, St. Mary's drainage and Swift Current drainage in Glacier National Park in Montana. The Glacier Park studies were made during the summer of 1925 and included a number of lakes and streams. The results as far as the lakes of Glacier Park are concerned are to be published in a separate paper. Data pertaining to streams are, however, incorporated in the present paper rather than in a separate account.

Acknowledgments. In Yellowstone Park the writer was variously aided by different persons, notably Dr. Gilbert M. Smith of the University of Wisconsin, and more recently of Stanford University (see collaboration, Muttkowski-Smith, the Food of Trout Stream Insects in Yellowstone National Park, in the Roosevelt Wild Life Annals, Vol. 2, No. 2), Mr. Alvin G. Whitney of the Yellowstone Park Forest and Trail Camp, Mr. E. R. Warren of Colorado Springs, Colo., and his assistant Mr. Ellis L. Spackman. Mr. Horace M. Albright, the Superintendent, facilitated the work by granting certain special permissions. Mr. M. P. Skinner, then Park Naturalist, and the rangers of the Tower Fall Junction Ranger Station assisted in various practical ways and by suggestions as to favorable localities. Above all, I am indebted to Dr. Charles C. Adams, until recently Director of the Roosevelt Wild Life Forest Experiment Station for many suggestions and direct aid; and to Mr. Howard H. Hays, then President of the Yellowstone Park Camps Company, for many courtesies, conveniences, and facilities, without which this study would hardly have been possible. To the present staff of the Roosevelt Station I am indebted for the laborious task of preparing this paper for the press and seeing it through.

To the Zoological staff of Cornell University I am indebted for identifications of various specimens: Dr. Needham and Dr. A. Claassen identified the Perloidea, Dr. Needham the Ephemeroidea, Mr. C. K. Sibley the Trichoptera,

Dr. A. O. Johannsen the Diptera, and Mr. H. Dietrich the Coleoptera. Most of the insects were in the nymphal or larval stages and the task of identification was therefore none too easy. To all these specialists I wish to express my grateful acknowledgment.

In general, the plan of the present paper follows that of an earlier one, the Fauna of Lake Mendota (Muttkowski, '18). That plan has received the sanction and approval of a number of ecologists, so that I do not hestitate to repeat it in the present study although slightly modified.

MOUNTAIN TROUT STREAMS

Classification of Mountain Trout Streams. Trout streams are highly aerated streams, found most abundantly in mountain regions. In the plains there are many "meadow" streams which also contain trout. These, however, are only of secondary interest here, since they are rare in mountainous regions.

Trout streams in Yellowstone Park and elsewhere in the Northwest can be broadly classified into three groups, according to certain physical characters:

a. *Constant streams,* with large amounts of water, which are, relatively speaking, only slightly diminished in summer. This group comprises the larger streams, such as Yellowstone River (Fig. 53), Gibbon and Firehole rivers in Yellowstone Park; the Snake, Boise, Clearwater (Fig. 54), Salmon, Coeur d'Alene and other larger rivers of Idaho; the Flathead and St. Mary's rivers in Glacier Park.

b. *Variable or flood streams,* which carry enormous masses of water for brief periods in the spring, due to melting snow, and then rapidly recede to one tenth or less of their flood level. These streams contain many rapids and in flood period may attain a formidable size. As examples may be mentioned the Lamar (Fig. 55), Gardiner, and Firehole rivers in Yellowstone Park, the forks of the Elk and Clearwater rivers and the Oro Grande (Fig. 56) and Palouse in Idaho and Washington, the Two Medicine River, MacDonald Creek and Swiftwater Creek in Glacier Park.

c. *Precipitous or cascading streams,* with many falls and rapids. Like the foregoing they are raging torrents during a brief spring, after which they shrink to unimpressive proportions, indeed, often to little more than mere trickles. This type is abundant throughout the Rockies. For the Yellowstone Park, I may cite Soda Butte Creek, Deep Creek, Broad Creek, Hellroaring Creek, Lava Creek, Lost Creek, etc. Tower Creek (Fig. 57) is an intermediate between *b* and *c*, but faunistically like *c*.

Yellowstone Park contains another stream which is unique and the sole representative of its type. This is Slough Creek, which consists of several tiers of meanders, and is located in the northeast corner of the Park (Fig. 58). There one finds splendid meadows, several miles in length, through which the stream meanders placidly (Fig. 59). The stream leaps from one meadow to the next through short but magnificent gorges. But the chief characteristic of the stream is probably glacial in origin; for the meanders consist of a series of deep holes, lined with huge boulders, which are connected by the quietly flowing stream. The rapids are confined to the gorges. In the "holes" or quiet pools one finds some of the largest trout in the Park.

Other mountain streams may course through long meadows and form meanders; but the "holes" are only occasional and do not consist of a series of depressions such as one finds in Slough Creek.

d. *Temporary streams, or snow flood streams.* These are not trout streams at all, but are included on account of their physical rather than biological relationship. This type includes the precipitous cascades and trickles that arise from melting snows and which for a time may carry considerable quantities of water, but which diminish to weak rills by the middle of summer and freeze up com-

Fig. 55. Junction of Yellowstone and Lamar rivers at low water stage. View downstream; Yellowstone River at left, Lamar entering at right. In spring the boulders in the foreground are under water. Sept. 5, 1921.

Fig. 56. Oro Grande River, Idaho. About 300 yards above its entry into the Clearwater. Showing rapids and boulders. In spring all except the largest boulders are covered by water. Aug. 31, 1924.

Fig. 57. Tower Creek, above the canyon, Sept. 6, 1921.

Fig. 58. Slough Creek, showing connected pools. The placid surfaces indicate the pools, the riffles indicate the gentle rapids connecting them. Photograph taken just above gorge, through which the creek enters the Lamar River. Aug. 11, 1921.

pletely in the fall (Fig. 60). Snowstorms and summer blizzards may give these streams a temporary prominence (Fig. 61). They become conspicuous as the snow melts, and the noise of their torrential fall can be heard at great distances (Figs. 62, 63, 64). Quite generally they end in sumps or swamps on the mountain sides or at the base of the slopes. Despite their temporary existence they have a fauna and a flora; and their terminal sumps supply abundant habitats for the early summer plagues of mosquitoes so common in mountain regions.

In selecting streams for comparative study it was essential to consider local convenience, accessibility, and type of stream. Four were selected for their location near Camp Roosevelt, which was used as a base. It would be difficult to find another point in the Park so favorably located, with representative types of so many kinds of streams all within convenient walking distance. After a preliminary survey, the following were chosen for intensive study: Yellowstone River, Lamar River, Tower Creek, and Lost Creek.

Yellowstone River was chosen to represent the first type, the large "constant" stream. The river is less than a mile distant from Camp Roosevelt and offers many ideal habitats on both sides of the Cooke City Road bridge, within convenient distance.

Lamar River was selected to represent the second type, the variable or flood stream. The Lamar joins the Yellowstone about three miles from Camp Roosevelt, and about a mile below the Yellowstone bridge. Excellent habitats were found in the gorge and eddies (Fig. 65) within the first few miles above the junction.

Lost Creek, although containing no fish at all, was selected for its accessibility and to represent the cascading or precipitous type of stream. It passes right through Camp Roosevelt, and its biota typifies such streams as Lava Creek, Tower Creek, Buffalo Creek, Blacktail Deer Creek, Hellroaring Creek, etc. Care was taken to check up Lost Creek frequently with Tower Creek, the fourth stream.

Tower Creek at Tower Fall is about two miles distant from Camp Roosevelt. But since it is much frequented by campers for about three miles above the mouth, the distance to the undisturbed sections made it rather inconvenient for frequent study. Besides, Lost Creek, as already noted, showed a practical identity of biota; hence one trip a week was considered sufficient for the study of Tower Creek.

The fauna of each type showed marked individuality. The work of comparison was begun at a favorable period, just preceding the summer emergence or transformation of insect forms. This seems to follow shortly after the spring flood period. Later on, after the first six weeks, as opportunity offered, hurried studies were made of other streams for comparison, such as the Gardiner and Firehole rivers, Lava Creek, Blacktail Deer Creek, Carnelian Creek, Elk Creek, Pelican Creek, Plateau Creek, and Buffalo Creek on the Lamar and Yellowstone rivers. Three days were also spent in a study of the biota of Yellowstone Lake, particularly in its relation to Yellowstone River.

Description of the Type Streams. a. *Yellowstone River.* The Yellowstone River arises far south of Yellowstone Lake. For the purpose of this paper only

the stretches below the lake are considered. After leaving the lake, the river is rather broad and in numerous places tends to become shallow and swampy, particularly on the right shore. Notwithstanding the swift current, considerable vegetation is present, such as *Myriophyllum, Ceratophyllum,* some *Potamogeton,* and the plumes of algae (probably *Cladophora*). This is confined to the lateral, quite shallow portions of the stream. In the adjacent swamps *Castalia, Nymphaea* and other swamp plants attempt to invade the stream, with little success.

About a mile above the Upper Falls the current increases its speed and plants become very rare, except *Cladophora,* which persists nearly to the brink of the falls. Just below the mouth of Alum Creek the river bed narrows and the shores become higher and steeper. The water, till then smooth and silent, now becomes turbulent, noisy and streaked with foam. Entering a short, rocky canyon, the river leaps over the brink with a vertical drop of 109 feet, forming the Upper Fall.

Here the aspect of the shores changes. For the Grand Canyon has begun, with its multitude of colors, its precipitous "needles" and rocks, its gay slides of sulphur sands—all thrown together in fantastic design. For twenty miles the canyon extends, with alternating areas of strangely colored formations and bluish gray cliffs (Figs. 66 and 67).

A third of a mile below the Upper Fall, the river takes a second leap of 308 feet, the Lower Fall (Fig. 68). The river then plunges into a series of cataracts, rapids and lesser falls, for a distance of twenty miles, or the length of the Grand Canyon. The total descent from Yellowstone Lake to this point is from 7740 to 6400 feet elevation.

A short distance above Tower Fall the canyon flattens out and the river becomes more placid. Tower Creek marks the entry into the Lower Canyon ("The Needles." Fig. 69). Here the shores are formed of steep, blue-gray cliffs, interspersed with minor slides of gayly colored sulphur sands. Below this is the Cooke City Road bridge (Fig. 70). Beyond the bridge the river is a series of rapids and eddies, winding between low and high hills, with occasional gorges and short canyons.

The sound of the river is a dull roar. If one approaches it—be it on a low shore, or between high cliffs—one may feel quakes and tremors of varying violence, giving one a curious feeling of uncertainty. Combined with this is the stench of the river, of sulfuretted hydrogen, like foul eggs, due to the masses of sulphur carried, and still more to the innumerable hot springs, small geysers, and mud swamps along the shores. The sulfuretted odor and taste of the water is never quite absent from the river; indeed, fish taken from the Yellowstone River have a strongly sulphurous taste.

b. *Lamar River.* The Lamar River drains practically the entire northeastern section of Yellowstone Park. More specifically, to the west and south it drains the watershed between the Lamar and Yellowstone rivers and Yellowstone Lake. To the east, it collects the waters from the Absaroka Range. For the greater part it flows northwest, its bed lying in a basin between the foothills of the Absarokas to the east, Specimen Ridge and Mirror Plateau to the west, and a series of peaks to the south, including Pelican Cone, Mt. Chittenden, Cathedral Peak, and Pyramid Peak.

Fig. 59. Slough Creek meadows. Aug. 29, 1921.

Fig. 60. Smaller Peak northwest of Lake MacDonald, Glacier National Park, showing the beds and confluence of temporary streams. While upper parts are dry, the streams still contain water at the confluence. Aug. 16, 1925.

Fig. 61. Mt. Brown and others, Glacier National Park. Taken from Lake MacDonald, after a summer blizzard. Aug. 15, 1925.

Fig. 62. Temporary stream resulting from summer blizzard; photograph taken on mountain slope, about 2500 feet above Lake MacDonald, Glacier Park, Aug. 17, 1925.

In its northward course it is joined by dozens of rills and creeks. Thus, on the left it receives Cold Creek, Willow, Timothy, Clover, Flint, Opal, Amethyst, Jasper and Crystal creeks; on its right it receives Miller, Calfee, Cache, Soda Butte and Slough creeks. Of these, Slough Creek and Soda Butte Creek are the most important tributaries.

Lamar River has no conspicuous falls or cascades, but drops steadily and gently from 7500 feet elevation at its point of entry into Yellowstone Park to 5800 feet at its junction with the Yellowstone. It is a beautiful stream, never very wide, with alternating placid stretches and gentle rapids. At points where tributaries enter, it widens and becomes turbulent, since most of the tributaries are precipitous and the force of their waters impound those of the Lamar, causing eddies, lateral gorges, and roaring rapids.

During the spring flood the Lamar rises to formidable heights. On June 20, 1921, the flood waters covered the rocks shown in figure 71 (see also Fig. 55). Examination of stranded débris indicated that the waters had been several feet higher during the preceding week. Even then the river was spectacular, both in appearance and sound—so much so, that as one stood on the point above its junction with the Yellowstone, the question suggested itself, "Does the Lamar feed the Yellowstone, or the Yellowstone the Lamar?" The Lamar seemed to carry a greater volume of water at the time.

A few days later, June 25, the river had fallen considerably, the boulders noted in figure 71 being wholly exposed. By July 16 the stream had fallen to the level noted in the photograph. The total drop was approximately fifteen feet.

Following the quick recession of waters, the Lamar forms an ideal habitat for *Cladophora;* the whole river bed is covered with the green streamers, so that from an elevated point some hundred feet away the waters appear a brilliant green. With the recession a very marked silting occurs in the shallower places, which has a striking effect on the stream life (Fig. 72).

c. *Lost Creek.* This is a typical mountain creek, carrying large quantities of water for short periods, and gradually shrinking to an unimpressive trickle, with perhaps less than one-fifteenth of its flood volume. Its main drainage is from the northern slope of Folsom Peak. Its banks are, on the whole, steep but not high. Smaller beaver works (Fig. 73) occur for six miles above Camp Roosevelt. There a series of small pools is connected by trickles, with beaver dams impounding the scant waters.

Lost Creek is not a trout stream, but its fauna and flora are typical of the smaller trout streams. For a short distance above its falls it becomes quite precipitous. It enters a short gorge, then tumbles over a cliff about sixty feet into Lost Creek Canyon (Fig. 74). Its bed then comprises shattered rocks, and some fair-sized boulders (Fig. 75). Over these it rushes in a series of steep cascades. At the base of the hill it spreads out in a delta and then disappears (Fig. 76) into the ground for several hundred yards—hence the name "Lost" Creek. It reappears along the Cooke City Road, which it parallels for about 500 yards down to Yellowstone River. Here it flows over a series of shelves, which in 1921 formed the site of a beaver colony, which was abandoned in 1922.

d. *Tower Creek.* This creek drains the elevated plateaus between Mt. Washburn and Folsom and Observation peaks, with headwaters arising at an altitude of about 10,000 feet. In its course of about twenty miles it drops to 6400 feet at Tower Fall, just before it empties into Yellowstone River.

In general Tower Creek is about twenty feet wide, and sixteen to twenty-four inches deep, with clear, cold water. Its bed is composed of water-worn cobbles, from a few inches to a foot in diameter, with occasional larger stones or boulders five to ten feet in diameter. In its upper reaches the banks are flat and frequently spread out to form broad pastures and willow swamps (Fig. 57), with adjacent beaver works built around pools or springs. But the stream itself is unobstructed, although frequent attempts at damming are evident. In its course Tower Creek receives the drainage waters of innumerable springs, pools and swamps, as well as of hillside sumps.

About seven miles above its mouth it receives the waters of Carnelian Creek (Fig. 77), a narrow and shallow stream with considerable fall, which is used extensively by beavers for a series of remarkable works (See Roosevelt Wild Life Bulletin, Vol. 1, No. 2, pp. 187–221, and Roosevelt Wild Life Annals, Vol. 1, Nos. 1 and 2, pp. 13–191, for E. R. Warren's papers on the Yellowstone Beaver). Two miles farther downstream the hills approach each other, and the creek enters Tower Canyon, through which it threads for about five miles (Fig. 78), emerging in a short gulch which parallels the highway. Here the bed is strewn with large rocks, up to ten feet in diameter, over which the water cascades in a series of short, turbulent leaps. The gulch continues for approximately 150 yards, then twists sharply, and ends between the characteristic needles which mark the entrance to the Lower Canyon of the Yellowstone. There the creek plunges over the cliff for a fall of 132 feet, and after a turbulent passage of 100 yards, joins the Yellowstone.

CRITERIA OF MOUNTAIN STREAM LIFE

The biota of any environment is determined by physiographical and physiological conditions. Physiography deals with the structural aspects of the environment, physiology with the functional aspects. For the first of these there are two viewpoints:—that of the geologist who deals with topographical classifications, and that of the ecologist who classifies the environment in terms of habitats. Hence under Physiography both the topography and ecology of streams must be discussed.

Stream Physiography. *The Physical Environment.* Under this head the sources of the streams and the structure of the shores and stream beds can be considered.

Sources. The sources of water are primarily the melting ice and snows of the mountains, and secondly the innumerable hot (Fig. 79) and cold springs found in the Northwest. Besides these, many swamps, sumps, and ponds drain into the streams.

The Shores. Geologically Yellowstone Park is of mixed origin—igneous, volcanic, glacial and alluvial. This is shown in the character of the various shores

Fig. 63. Bed of hillside stream (temporary stream), with trickle of water from spring. Sandstone formation, Clearwater River, Idaho. Aug. 30, 1924.

Fig. 64. Bed worn in sandstone by temporary stream, Clearwater River, Idaho. Area burnt over by forest fire. Aug. 30, 1924.

Fig. 65. Lamar River eddy, looking upstream. To the left the high water mark of the spring floods shows clearly. In June the stone in foreground was completely covered by water. Sept. 4, 1921.

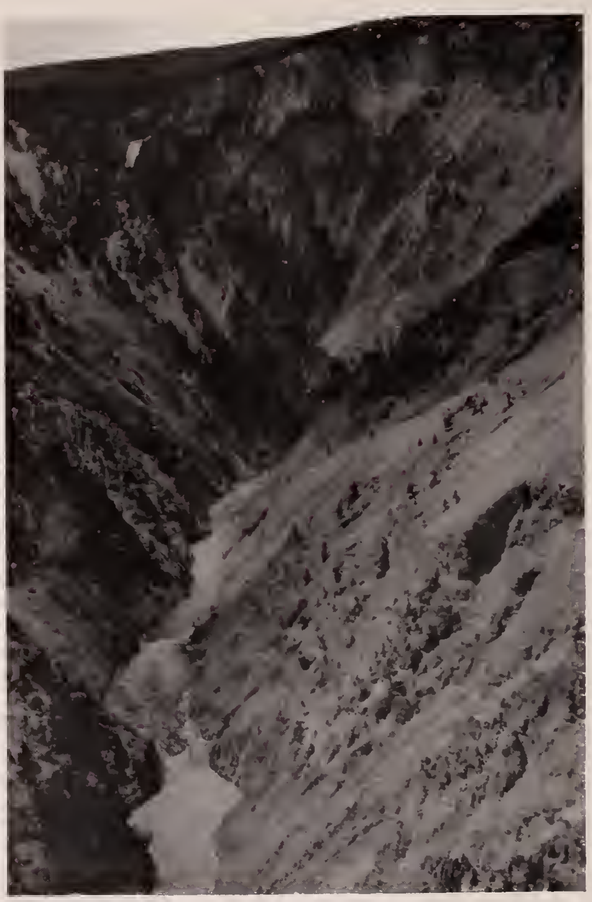

Fig. 66. Grand Canyon of the Yellowstone. Lower Falls at upper left. The characteristic "sulphur slides" to the right. Aug. 21, 1921.

and streambeds. Nearly every stream in the Park at some point or other passes through rugged canyons composed of basalt cliffs. Decomposed lava slides are frequent. Along the streams and on the uplands one finds numerous boulders left by glaciers (Figs. 80 and 87), while in places there are great accumulations of soil left by past floods. Much of the area in the region of Camp Roosevelt is thought to be the crater of a huge extinct volcano (Fig. 81).

A feature of the shores of mountain streams is the changes taking place, produced by two factors, (a) snow, and (b) the streams. The changes are slow but they are nevertheless easily recognizable. The streams for the greater part have eroded their beds considerably, so that the present shores are quite steep, even perpendicular in many places (Fig. 82). During the spring floods the present shores are undermined; this tends to produce land slides, which in turn, precipitated into the waters, affect the stream beds.

On the steep slopes the long winters deposit gigantic snow drifts, whose weight, pressing on trees, bushes and the loose earth, dislodges these and gradually forces them into the stream. During spring the melting snows may cause great sections of the shore slopes to slip into the stream. This is particularly true of Yellowstone River, where the slides are numerous, and the shores for many miles are quite declivitous (Figs. 66–68). It is also true for streams like the Lamar, Tower Creek, Lost Creek and many others. At many points along these streams there were signs of recent "slips" during the summer of 1921, and of others of older date.

In places the trees, shrubbery, and débris thus precipitated into the stream may become caught between or against protruding rocks and cause a damming of the stream. Jammed trees are frequent in the great rapids of western streams (Figs. 83 and 84).

Wintering animals, such as the Coccinellidae (Fig. 85), may be buried under the snow and later swept into the water by the snow slides. Others, including mammals such as buffalo, deer and elk, may become mired in the snow-drifts and are suffocated (Fig. 86); these, too, may be carried into streams by snow slides, since quite frequently one may find parts or whole skeletons of winter killed mammals in the streams.

THE STREAM BEDS. Change, too, takes place in the stream beds. The force of the spring waters in particular brings about many marked annual changes. The flood currents wash out all the lighter materials such as sand, mud, silt, and deposits on rocks, so that the bottoms appear clean-washed or scoured. Later with the recession of the floods, muck, silt, smaller pebbles and sand are deposited along the shores among the rocks.

In midstream the floods tend to fill up the pools. In turn, they may wash out new pools. Even during the summer, with water at lowest stage, and depending somewhat on the size of the stream, there is a constant movement of the bottom. Stones of varying size are displaced, ground together or battered against each other, and whatever living creatures may come between will be crushed. A water net, or still better, a plankton net, left in a stream just below some rapids, will collect abundant evidence of this fact in the way of crushed caddisworms, mayfly and stonefly nymphs, and occasional trout eggs and embryos.

The Ecological Habitats. Like other ecological units, the mountain stream may be subdivided into minor habitats, which can be readily recognized according to physical characters and the biota. These habitats intergrade, here as elsewhere. Following is a classification, based on comparative studies of the streams of Yellowstone Park and other regions of the Northwest:

1. Permanent habitats, with native (endemic) biota.
   a. White water habitats—falls, cascades, white rapids.
   b. Clear rapids and stone bottoms—on and under rocks.
   c. Placid water habitats—pools and holes.
   d. Marginal areas—on or under rocks, in soil.
2. Interrupted habitats, with native biota.
   e. Deposits—on rocks, bottoms, or shores.
   f. Splash areas—on rocks.
3. Temporary habitats—transient and transitional, with varied biota.
   g. Marginal pools.
   h. Recession areas.

The permanent habitats (1) are stable and are typical of the center of the streams; their plant and animal life varies but slightly the year round.

Interrupted habitats (2) are found both in the center and at the sides. The transient and transitional habitats (3) comprise relatively quiet spots, temporary in existence, that dry up in low water stage and are destroyed by high water. The biota in such areas is extremely varied.

PERMANENT HABITATS. As already noted, these comprise the central parts of streams; they offer the greatest degree of constancy in mountain streams. In such places one may find the same fauna and flora practically the year round.

a. White water habitats. As indicated by the name, these are characterized by foaming or "white" water. That is, here the current and the mass of water are sufficiently swift and great and the obstacles opposed to its flow sufficiently firm to batter it into a white foam. Such white water is that of falls, cascades, and major rapids. Falls (Figs. 66, 68, 74, and 88) indicate a vertical flow of water; cascades an oblique flow (Fig. 89); white rapids (Fig. 95) are a mixture of horizontal, oblique and vertical currents. In mountain streams all of these are intermingled. They constitute a highly specialized habitat, combining strong and twisting currents and highest aeration.

b. Clear rapids and stone bottoms. Here are included rapids of less violence, with fewer opposed obstacles, so that the water is transparent and one may readily see the bottom. Very characteristically the bottom in these rapids is nearly uniformly composed of rounded stones of various sizes (Figs. 87 and 90). But there may also be angular granitic rocks, and angular stratified rocks (Fig. 91). Thus, in the Yellowstone, all types of bottom may be found. At one point, just below the largest group of "needles" in the lower canyon, there is evidence of a formation similar to those of Mammoth Hot Springs; this formation tips into the stream and extrudes at low water stage. But the most common condition, which applies probably to more than 90 per cent of the stream beds, is that of rounded, water-worn cobbles (Fig. 57).

Fig. 67. "Sulphur slides" of Yellowstone Grand Canyon. Intermixed with these are "needles," which also are characteristic of the formations of Yellowstone Park. Aug. 21, 1921.

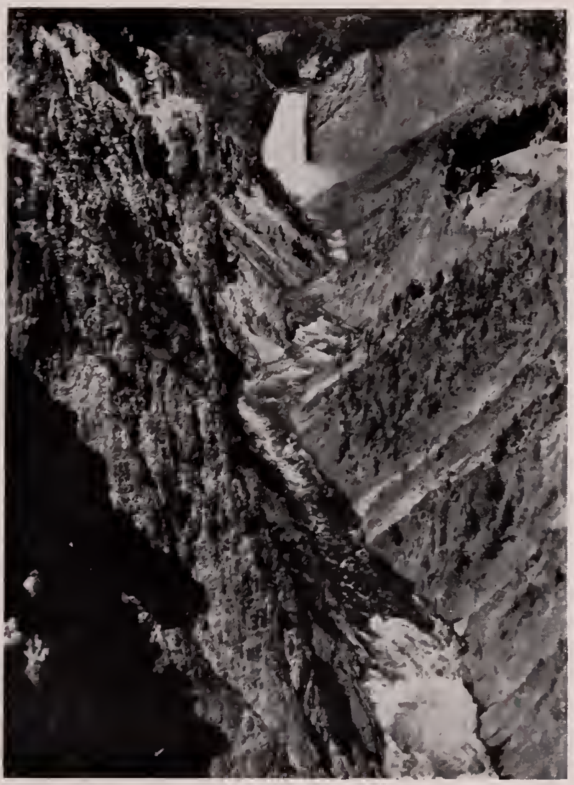

Fig. 68. Lower Falls of the Yellowstone and rapids. Note intermixing of "needles" and "slides." Aug. 21, 1921.

Fig. 69. "The Needles," looking directly across the Yellowstone in the Lower Canyon. Note the layer of basalt rocks near the top. Aug. 22, 1921.

Fig. 70. Yellowstone River at Cooke City bridge. Lamar River Valley in upper middle. Aug. 8, 1921.

c. Placid water habitats. These are the "holes" and "pools" in the beds of the streams and are of varying size. They may have been washed out by falls, gouged out by stones born along by the waters, or they may be of glacial, volcanic, or perhaps seismic origin. At the base of falls the pools are turbulent and belong to the "white water" habitats; otherwise they are relatively quiet at the bottom, since the current is strong only in the surface strata. Often such pools have a scanty floor of gravel, or a sandy bottom—deposits that have been made after the spring floods.

d. Marginal areas. The shores may comprise cliffs, boulders, or smaller stones, and are rarely sand, pebbles, and mud. Here the impact of the water is primarily lateral, not horizontal or vertical (Fig. 92). Friction by débris is marked. This is an area offering many shelters, but too often of only temporary nature. Many smaller organisms live under and between the rocks, while others live in the moist or wet soil.

Interrupted habitats. These comprise primarily the deposits (e) on the bottoms, shores, and sub-surface rocks. At first these were regarded as transient in nature, since the deposits are absent during the flood period and accumulate progressively during the summer. Still, one finds these deposits in mid-stream, often exposed to a fairly strong current, and covering the huge rocks that so often form the margin of the "holes" and pools. The deposits persist during the winter and only the scouring spring floods sweep them away. But during their existence they afford a habitat for numerous Chironomidae and rock diatoms. The deposits extend from mid-stream to the shore rocks. In Yellowstone Park they contain much sulphur sand.

f. Splash areas. These are the exposed rocks in rapids or along shores, which are continually moistened by spray. Almost any time during the year—spring, summer, fall, winter—one may find adult insects running up the rocks, flying into the spray, and once more running upward. They may be found chiefly on the downstream side of the rocks. Such are the Diptera, Trichoptera, and more rarely the mayflies (Figs. 93, 108 and 114).

Temporary habitats. These comprise (g) the marginal pools and shallows which are found during a large part of the year, and (h) the recession areas, following the spring flood. One might also refer to them as transitional and transient areas;—transitional as regards the biota, transient as regards their period of existence. They are the lesser shore rapids, which silt in quickly, and the marginal pools that appear with the recession of the flood waters. Later on the interstices between the stones become filled in with sand and débris (Fig. 94). Tiny rapids or trickles continue to fill in the connections, until the pools are completely separated. Often a series of marginal pools is thus formed. The trapped fauna either migrates or dies, and the temporary habitat becomes populated with invading biota. It is remarkable how quickly such a temporary habitat is invaded by aquatic beetles, water bugs, Chironomidae, Rotifera, Protozoa, filamentous algae, and scattering plankton Crustacea. All of these types come primarily from the swamps, sumps, pools, and springs found so abundantly in mountain areas. After a few weeks these places dry

up and with them the biota disappears. Or, if a pool is fairly deep and does not dry up completely, then the fall rise of the waters will wash away the invading biota and restock the pool with native forms.

Habitat Distribution. A striking difference between mountain streams and other water bodies such as lakes, ponds, and slow plains streams, is the absence of regularity in the arrangement of habitats. In mountain streams the habitats are all commingled; pools may follow falls, rapids alternate with eddies, marginal pools may adjoin cataracts. In other words, there is a complete absence of that regularity which permits a zonal classification for lakes, ponds, and slow streams. On the contrary, the contrasts are quick and startling, one extreme follows another. Hence in a very small area one may find all the extremes from a vertical to a horizontal flow of water, from shallow, placid stretches to deep, stone-lined pools. This, in a sense, is advantageous, since it permits the study of diverse conditions in a rather short time. A second advantage arises from this, namely, that the deeper portions of the stream approximate the flood conditions, while shallower places permit more intensive study of the biota and its relation to other communities.

In summary, there is in mountain streams only a horizontal distribution of habitats, no vertical. The habitats must be studied in horizontal order, not in the vertical order one finds in lakes and slow streams.

Stream Physiology. From a physical viewpoint, mountain streams are distinctive. Parallel with this is the functional or physiological aspect, with equally distinctive features, which depend upon extrinsic and intrinsic factors. The extrinsic factors are such as affect the stream as an entity, namely, the molar agents, including winds and currents, chemical makeup, temperature, and circulation. Intrinsic factors are those which affect the makeup of the flora and the fauna. These are currents, respiration, food supply, footholds, locomotion, and special habits.

Extrinsic Factors. MOLAR AGENTS (Winds and Currents).—Winds do not directly affect the mountain streams. Since the streams have bitten and scoured their beds deeply, the shores are usually high and the waters are therefore sheltered from winds. The rush of the waters, however, generates definite air currents (Fig. 95) which entangle with the shore-winds high above them and create vortices and treacherous back drafts which readily draw unwary insects and other winged life from their line of flight and spill them into the hurrying waters beneath. This results in the surface toll or "surface bait" of the summer months.

In the winter the surface winds carry snow into the gorges and canyons, piling it on the shores of their streams in huge drifts, to be dislodged by wind vortices or undermined from beneath. Avalanche after avalanche then crashes down the slopes, dislodging trees, boulders, or causing huge land slides into the streams. In the spring the melting snows are readily displaced by the winds and slide into the streams. For weeks after the snow has disappeared from the lower levels the streams are turbid from the sands and sediments washed along by the currents.

To a lesser extent the currents, especially during the flood periods, undermine the shores and cause slides. For it is noteworthy that most slides start from above and not from below.

Specifically, the currents are concerned with molding the bed of the stream, the winds primarily with molding the shores (Fig. 96).

CHEMICAL COMPOSITION. In general, mountain streams are noted for the purity of their water. This is true also for the streams of Yellowstone Park, except Yellowstone River and Firehole River. These two streams are both distinguished by a sulphury taste and odor the year round, rendering the water unpalatable and incapable of quenching thirst. Two factors seem to cause this: (a) The nature of the river shores and bottoms, from which masses of sulphur sand are constantly dissolved and swept along by the currents; (b) the innumerable hot and cold springs and geysers along the shores, which contain sulphur, and sometimes arsenic and other compounds. Some of the springs may rise from the river bed; hence they are submerged for a good part of the year and become exposed only during the low water stage of summer. The spring seen in figure 79 is of this type, and was exposed only when the water had dropped about twenty inches.

Practically all other streams in the Park carry considerable amounts of sulphur in suspension during the flood period and their waters are not very palatable and refreshing during that time. But as the waters grow clear, that is, as the sulphur sands have silted out, they improve in potability. Moreover, the fish then lose the sulphury taste they all seem to have during the flood period.

TURBIDITY. Due to the materials in suspension, most mountain streams are very turbid during the flood periods. Usually by the middle of July the waters become clear. Temporary turbidity, however, is quite frequent, and is caused by rains and by shore slides. Unless the rains have been very severe, the temporary turbidity lasts only a few hours. Where a mountain stream passes through large upland meadows, as is the case with the Gardiner River and Slough Creek in Yellowstone Park, the Clearwater, Oro Grande, Wietas, and Forks of the Elk River in Idaho, and the Flathead and St. Mary's rivers in Glacier Park,—the rains wash down considerable quantities of mud, and this requires a much longer time to sediment out than do the sulphur sands.

As a matter of fact, local turbidity occurs quite often, due to the dislodging of some rock by the current or some passing animal. This temporary and local turbidity seems to have the effect of making the moving fauna scurry into shelters.

AËRATION. The continuous and marked descent of waters in mountain streams results in a thorough churning and mixing of water with air, and hence in a high oxygen content. Oxygenation reaches its highest level in mountain waters since, besides the churning, the low temperature permits the absorption of greater quantities of oxygen.

TEMPERATURE. A characteristic of a mountain stream is the uniformity of its temperature. The constant churning and mixing does not permit a thermal stratification such as one finds in quiet streams, lakes, ponds and swamps.

Temperatures taken in Yellowstone River at the bottom of deep "holes," in eddies and in rapids, were all identical. There is a difference among streams, however. Small creeks such as Lost Creek rose rapidly in temperature; here the heat reflected from the slopes raised the temperature of the water as much as 8° C.

An interesting fact is that the waters of Yellowstone Lake, before passing into the outlet, absorb considerable heat from the sun. As a result, the river in later summer showed a higher temperature than the Lamar River, or Tower Creek. Streams that are fed by many springs do not freeze over in winter.

Circulation. In lakes, ponds and slow streams circulation is affected chiefly by winds and convection currents. As a result a thermal stratification is established and with it a stratification of dissolved gases. In mountain streams circulation is direct and complete. The constant descent of water results in a thorough mixing, so that both temperature and oxygen content are equalized throughout all parts of the stream. This is one of the most marked physiological differences between mountain streams and other aquatic bodies.

In summary, current caused by the descent of water is the primary extrinsic factor, which in turn affects the aeration, temperature, circulation and transparency of the stream.

Intrinsic Factors. Except for certain Tipulidae larvae burrowing along the shores among rocks, the primary fauna of trout streams is confined to water breathers, i. e., such as obtain their oxygen from the water. The speed of the current precludes any sort of emergent vegetation, which latter is essential for surface breathers, i. e., breathers of atmospheric air (see Muttkowski, '21). Among animals, therefore, only such as breathe oxygen in solution in the water are found—in general, only such types, especially among insects, as require a high degree of oxygenation.

Because of the currents, the biota is further limited to species that are either strong swimmers or strong clingers—the latter directly by means of structural adaptations (claws, suckers) or indirectly by means of clinging devices constructed by the various species (webs, jellies, attached cases).

The current causes a third limitation, namely, in the matter of food supply. Species living here cannot limit themselves to plant or animal food, or as in quiet habitats, to some one particular type of plant or animal. On the contrary, favorable locations here are more isolated—"biotic islands," one may say, where a few plants and animals assemble; and a hungry specimen must eat whatever is available. Indeed, one finds that habitually carnivorous and herbivorous species both become mixed feeders in mountain streams. On the whole, the highly specialized conditions call for specialization in structure, but for generalization in diet.

In summary, the current and resultant high oxygenation are the dominant intrinsic factors which affect the physiology of a stream. These at once limit the biota (a) to water breathers, (b) to active swimmers and clingers among water breathers, and (c) to indiscriminate feeders, i. e., species of unrestricted diet.

A further restriction arises from certain special habits. As noted in a previous paper (Muttkowski, '18, p. 386), a special habit may eliminate a species

Fig. 71. Rocks at eddy of Lamar River. Low water stage. In June these were completely covered by the floods. Sept. 4, 1921.

Fig. 72. Stream bed of Lamar with recession pools. Aug. 8, 1921.

Fig. 73. Beaver pond on Lost Creek, showing hut in middle. June 26, 1921.

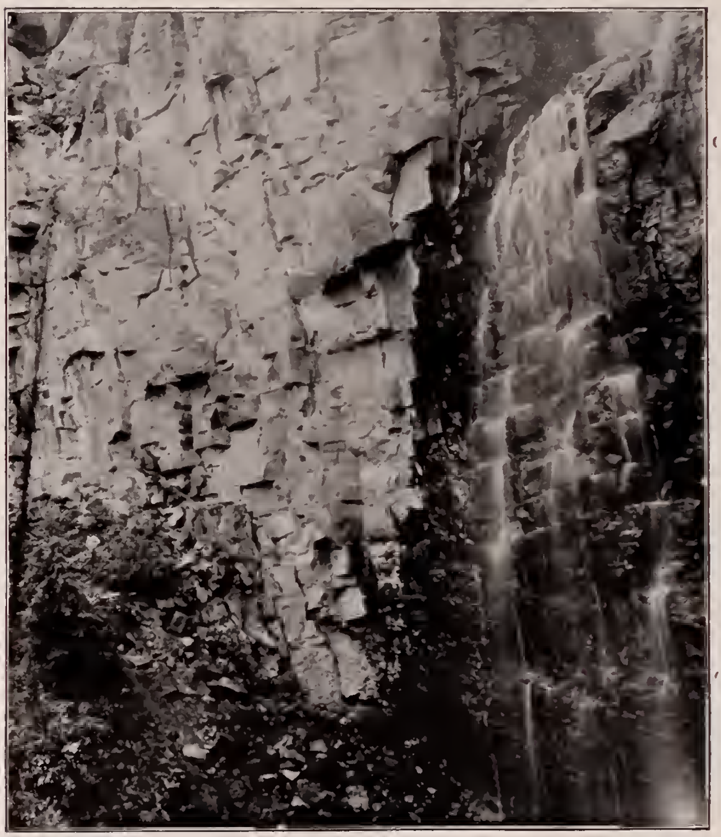

Fig. 74. Lost Creek Falls. Sept. 2, 1921.

from a habitat which it might otherwise inhabit. This was instanced by Odonata, many of which deposit their eggs on or in emergent vegetation. Where such plants are absent, these Odonata will not be found, although they are water breathers.

QUALITATIVE LIST OF PLANTS AND ANIMALS

The following lists cover only the more dominant or "type forms" of mountain waters. No attempt was made to secure a complete collection of the species: only enough to ascertain the dominant types, to learn something of their relations to the environment, and of their interrelations with one another. Further, only the native biota is considered. Attention has already been directed to the ecological distinction between primary and secondary inhabitants, or between native and invading species. Such plants, for instance, as *Elodea, Nymphaea, Castalia, Potamogeton*, may occur at some rare point in a mountain stream, where for some reason or other the current is greatly diminished and permits a slight amount of plant growth. But such single occurrences hardly warrant their being listed as native species.

A further restriction must be noted because of the taxonomic difficulty. This arises from the fact that in so many species one deals with immature stages, many of which are as yet unknown to taxonomists. This fact was realized long before these studies were begun. In the Park a distinct and prolonged effort was therefore made to secure complete "life histories" of many insects. In fact, I tried to breed many stages. Cans and jars, partly filled with stones and covered with cheese-cloth, mosquito bar or wire screening, were placed at advantageous points in Lost Creek, where human intruders were rare. Alas! While my security from humans proved complete, I had not anticipated the insatiable curiosity and impish destructiveness of the bears. Day after day, despite my best efforts in hiding my experimental jars, the bears searched them out and despoiled or destroyed the jars and their contents. This lasted for more than four weeks, after which I surrendered to the superior patience of the bears.

This is not offered as an excuse, but to signify a real condition that confronts the investigator at times in Yellowstone Park. Visitors in the public camps frequently use the streams to refrigerate some of their food supplies during the night. This the bears seem to know and very often seek out the "caches" for a toothsome morsel. Some of the bears are known to plunder the food boxes which campers carry in their cars or on the running-boards. Being possessed of curiosity, the bears would quite naturally seek to know what was hidden in the jars I had planted in the stream bed. The results were disastrous so far as my breeding experiments were concerned.

In view of this, I tried so far as possible to secure representatives of various stages of insects, to be associated later on if possible. Such a method is unsatisfactory, of course. But under the circumstances it offered the nearest approach toward securing complete life histories.

The Plants. The list of plant species given below is copied from Muttkowski and Smith's, The Food of Trout Stream Insects in Yellowstone

Park (Roosevelt Wild Life Annals, Vol. 2, No. 2). This list was based on certain surveys made for the purpose of checking the food available in given localities with that actually eaten by insects found in the same places.

A marked characteristic of mountain streams is the total absence of higher plants. Lower plants, too, when present at all, are none too conspicuous and generally are confined to one or two forms of algae. When these occur, they are present for only short periods. Thus, *Cladophora* was found in the Lamar River in considerable quantities for about four weeks; the entire bed of the stream was decorated with bright plumes, so that from a distance the water appeared a bright green. But in about four weeks most of this luxuriant growth was gone and the remainder was a sparser and shorter growth of *Cladophora*.

The same held true for the Gardiner River. In Yellowstone River *Cladophora* was very scarce, an occasional plume occurring in some sheltered or less exposed spot. In Tower and Lost creeks, also, for some unexplained reason (perhaps due to lack of carbonates), *Cladophora* was scarce. On the other hand, in Lost Creek, Tower Creek, Lava, Blacktail Deer, Hellroaring, and other creeks, the flat *Prasiola* was fairly abundant and associated with a type of *Nostoc*. This same scarcity of *Cladophora* was noted in 1925 in the streams and lakes of Glacier Park.

Besides *Cladophora*, smaller filamentous algae and various diatoms thrive among the small accumulations between rocks; this includes such forms as *Melosira*, *Ulothrix*, *Closterium*, *Cocconeis*, etc. In the marginal pools *Spirogyra* may thrive temporarily.

Following is the alphabetical list:

Cladophora sp.	*Nostoc* sp.
Closterium sp.	*Oscillatoria* sp.
Cocconeis sp.	*Prasiola* sp.
Epithemia sp.	*Rhoicosphenia* sp.
Gomphonema sp.	*Spirogyra* sp.
Melosira sp.	*Synedra* sp.
Moss—undetermined.	

An occasional battered fragment of *Potamogeton*, *Chara*, or other lake plant might also be found in Yellowstone River, washed down from the lake.

The Animals. The specialized conditions of mountain streams restrict the number of animal species very markedly. In Yellowstone Park only three of the Phyla can be called endemic, namely the Platyhelminthes, Arthropoda, and Chordata. For Idaho, Washington, and Montana, certain additional phyla can be noted—at least for some of the streams. Besides these representatives of other phyla are of sporadic occurrence.

a. *Invertebrate Phyla (exclusive of Arthropoda)*. 1. PROTOZOA.—Only the Vorticellidae and the parasitic *Gregarina* can be considered as native in the quick-flowing mountain streams. One finds them more frequently, however, in the marginal and sheltered pools left by receding flood waters. Where the current is strong they do not occur, as a rule. Occasionally, where small masses of filamentous algae, e.g., *Cladophora*, *Melosira*, *Oscillatoria*, etc., have become

Fig. 75. Lost Creek, low water stage. In June all the stones were covered by water. Sept. 2, 1921.

Fig. 76. Lost Creek, low water stage. Showing the last pool in the bed of the stream. The stream is dry for nearly a hundred yards above this point. Sept. 2, 1921.

Fig. 77. Tower Creek, confluence with Carnelian Creek (right). Sept. 6, 1921.

Fig. 78. Tower Creek in Tower Creek Canyon, showing the thickets along banks and stones in bed of stream. Aug. 14, 1921.

wedged between rocks, or have formed accumulations at stagnant points, various Protozoa do occur, such as the ubiquitous *Vorticella, Paramecium,* several species of *Ameba, Oxytricha, Colpoda,* etc.

A second condition under which one may find the Protozoa in rapid waters is within the shelters formed by other animals, such as the cases of Trichoptera and the tubes of Chironomidae. Here they may lodge, or attach themselves to the occupant, a habit that applies particularly to the Vorticellidae. Empty cases and tubes often contain a surprisingly varied microscopic life.

Among the deposits on stones, particularly those of the "holes," the Vorticellidae frequently form colonies of considerable size, numbering many thousands of individuals.

Perhaps most surprising is the wide occurrence of *Gregarina* in the various aquatic insects, especially in Trichoptera. As noted in a second paper (see Muttkowski-Smith), the specialized conditions of the habitat force a generalization in diet. It seems that insects and other animals are readily crushed, and such fragments are avidly eaten by nearly all the different insects inhabiting the mountain streams. Frequent catches made with plankton nets demonstrate this fragmentation clearly. It is by eating these fragments that insects spread the *Gregarina* among themselves; for certainly the *Gregarina* are entirely passive in this matter.

2. Porifera, Coelenterata. Neither sponges nor hydrozoans are found in the rapid waters, although they are of frequent occurrence in adjacent ponds and small lakes. In European mountain streams several species of *Hydra* have been noted in very placid stretches of their waters. These species can hardly be considered as native.

3. Rotifera. Rotifers are of sporadic occurrence, being usually found together with Protozoa in mats or wads of filamentous algae. Their occurrence seems chiefly accidental. Insects feeding on the algal mats will readily devour the rotifers and other small animal life. In the larger streams of the Northwest, such as the Snake, Clearwater, or St. Joe, one may find Rotifera in quiet stretches, especially where the streams pass through great meadows.

4. Platyhelminthes. Two species of flatworms are very typical of the western mountain streams, namely, *Polycelis nigra* Ehr., and *Dendrocoelium lacteum* Mueller. The black *Polycelis* is very common, the white *Dendrocoelium* much less frequent. The larger the stream, the less the abundance of these flatworms. The optimal habitat seems to be that of moderate sized streams. In Tower Creek most of the stones had numerous specimens on their under sides, where the worms moved rapidly on their slime trails, feeding on the various rock diatoms growing there and on the shore diatoms swept along by the current and caught in the slime films. They reach a length of about 18 mm.

The scarcity of flatworms in Yellowstone River may possibly be due to the great amount of sulphur carried by the stream. Still, Tower Creek and Lost Creek both carry large quantities of sulphur, at least during the flood period. On the other hand, the small number might be explained on the basis of too strong a current. But here again it must be noted that comparatively speaking the current in Tower Creek is faster than that of the Gardiner and

Lamar rivers; yet Tower Creek is an ideal stream for flatworms and they occur there in multitudes. In fact, in Lava Creek, which is still more rapid, the flatworms are even more abundant.

5. NEMATHELMINTHES. Except for a parasitic *Mermis* sp. found in *Simulium* larvae and mayfly nymphs (Fig. 103), and an occasional *Gordius* larva, the round worms and hair worms are absent. Thienemann finds that *Mermis* and *Gordius* in their last or adult stages like to burrow in the wet soil at the margins of spring-fed pools and also among the deposits on rocks.

6. MOLLUSCA. To my surprise I did not find any snails or clams represented in any of the mountain waters. This is contrary to the findings of Steinmann for Switzerland and of Thienemann for Germany. Not even the univalve *Ancylus* was noted. Only in quiet stretches where the streams flow through the higher meadows, do occasional *Planorbis* and other snails occur.

7. ANNULATA. Annulate worms and leeches seem to be entirely absent from the streams examined in Yellowstone Park. Only one specimen of a *Pristina* was found on August 31 in Yellowstone River. Very probably this came from an egg that had floated down from Yellowstone Lake. In this respect the larger streams of Idaho show some difference. Thus in the Clearwater and Snake rivers an annulate, probably a *Limnodrilus*, is quite abundant in the clear rapids. Leeches, too, occur in the Clearwater, under the shore rocks. These shores recall the lake shores markedly, since similar species occur in both, e. g., leeches, flat mayfly nymphs (*Heptagenia* sp., etc.), *Psephenus* (Fig. 115), flat Trichoptera cases, hydroptilids, etc.

b. *Arthropoda*. The Arthropoda contain the dominant forms of the mountain streams which could be studied more carefully in their interrelations.

1. CRUSTACEA. Crustacea are conspicuous by their absence from the mountain streams of the Parks, Yellowstone and Glacier. Yet in the large trout streams of Idaho and Washington, such as the Clearwater, St. Joe, Spokane, the St. Mary's in Montana, etc., one finds *Cambarus* quite frequently, and occasionally *Hyalella* and some forms of *Gammarus*. Smaller plankton Crustacea, too, may occur. This distribution in Idaho may be due to the greater amount of mud present in the streams, and the many long placid stretches where the streams move through the "upland meadows." Perhaps the lower altitude (3000 ft. and less in the places examined), may have something to do with the Crustacean representation. Thienemann calls attention to the fact that the chemical composition of the waters, particularly the carbonates, affects the faunal composition in very marked manner. It is possible that the paucity of Crustacea and Mollusca in the Park streams is to be associated with the presence or absence of the carbonates. Unfortunately, I had neither the time nor the requisite equipment to determine this.

From the parasitic viewpoint also the Crustacea do not seem to be established in the Park. Of the several hundred trout examined only one was found to have a copepod gill parasite.

2. ARACHNIDA. Shore and rock spiders were observed quite commonly in their hunts along the stream. Their main prey seemed to be the adult caddisflies. On overhanging rocks, on the bridges, and on trees along the shores,

webs of other species were found which contained caddisflies, mayflies, and smaller stoneflies (Figs. 97 and 98). Such webs are often nothing more than irregular tangles of silk, anchored here and there, but not stretched out in any regular fashion. The spiders seem to be able to run on the surface film of the water for short distances. Thus, on September 1 a number of spiders were observed on Tower Creek, running close to the water, or even skating out on the surface film after caddisflies.

These spiders no doubt account for a considerable number of adult aquatic insects. The caddisflies formed by far the major portion of the web contents. In turn the spiders occasionally fall prey to the current and are eaten by the fish.

Hydrachnida, like the Protozoa, Rotifera, Mollusca, and Crustacea, are not native in the mountain streams of Yellowstone Park. In the smaller streams they are sporadic, usually where a slight tendency to swampy conditions manifests itself. In Lost Creek I found Hydrachnida in beaver ponds. In the Lamar they occurred in empty Trichoptera cases and among the mosses in very shallow water. Both Steinmann and Thienemann record a number of species for the streams of Europe.

3. INSECTA. *Perloidea.*—The stoneflies form the dominant invertebrate animals of the mountain streams. While they also occur in other aquatic bodies, such as lakes, ponds, and slow streams, their optimal habitat is rapid waters, particularly the cold mountain streams, with rapids, cascades and falls and therefore with a high degree of oxygenation—precisely the type of waters preferred by trout. One may say that trout and stoneflies are intimately associated; where one occurs, the other also is found.

In Yellowstone Park about a dozen species were captured; and of these about five were numerous and conspicuous, the remainder occurred more sparingly. In habitus the larvae are very dissimilar, a fact which correlates with their habits and habitats. Thus the largest species, *Pteronarcys californica* (Fig. 99), is conical and long, the sulphurous *Acroneuria pacifica* short and squat, with *Acroneuria theodora* intermediate in shape, somewhat short, but less markedly flattened. This divergence in shape is associated with divergence in habits. *A. pacifica* is primarily a clinging species; it hunts the undersides of rocks in strong rapids. *Pteronarcys californica* is a roving type, and hunts between rocks; it migrates freely from pools to rapids, and from midstream to the shores in search of food. The various species of *Alloperla* are elongate, only slightly flattened, and are found at the bottom of pools or "holes" where the surface current sweeps above them and leaves the bottoms relatively undisturbed. They, too, are rovers.

Following are the species determined; *Pteronarcys californica* Newport, *Pteronarcella badia* Hagen, *Perlodes* Hagen, *Acroneuria pacifica* Banks, *Acroneuria* (*Donoroneuria*) *theodora* Needham and Claassen, *Perla verticalis* Banks, *Isoperla 5-punctata* Banks?, *Alloperla coloradensis* Banks, *A. lineosa* Banks, *A. fidelis* Banks, *A.* sp.

Of these *Pteronarcys californica* is most conspicuous, by virtue of its size and bright salmon color, although it is really less numerous than its sulphur-

colored relative, *Acroneuria pacifica.* This, the largest of stonefly species, has received a number of popular or local names, according to color, region, shore vegetation, and the kind of fish found; thus one meets with names such as salmon flies, trout flies, mountain flies, red flies, river flies, willow flies, grass flies, etc.

The larvae attain a size of three to three and one-half inches (Fig. 99). In color they are a dull blackish gray, with yellow or orange dorsal and lateral stripes. Their form is conical, widest at the thorax and narrowest at the caudal end. They are good swimmers, but move mainly by creeping among the rocks in the weaker rapids, eddies, and bottoms of pools. Strange to say they eat plant food almost entirely, differing in this respect from other perloid nymphs. Thus, the stomach contents of both young and full grown nymphs were diatoms, bits of algae, wood, and bark, while those of other stonefly nymphs were chiefly animal matter. The roving habits of this species make it a favorable food item for trout, more so than any other perlid species.

Transformation appears to coincide with the recession of the spring floods, when the waters are still turbid and a Secchi's disk is visible for scarcely ten inches. In 1921 transformation began on July 5 at the Cooke City Road bridge (Fig. 70) over the Yellowstone, and lasted for about a week, although some belated stragglers continued to emerge till July 26. But the peak of transformation was July 5 to 8. Curious to say, the transformation at this point did not coincide with the upstream and downstream emergence. Upstream, in the stretch of river between the lake and Upper Falls and in Yellowstone Lake final ecdysis was pronounced from June 25 to 30, according to reliable information received from Mr. Ainesworth, of the Lake fish hatchery. Downstream, at the eddy at the mouth of Elk Creek, this species transformed in large numbers on July 15 and 16. Opposite Hellroaring Creek transformation was very pronounced on July 19 for both this species and *Acroneuria pacifica.* Visitors at Camp Roosevelt from points north of the Park reported that large numbers were emerging on July 21, along the Gardiner-Livingston highway which parallels Yellowstone River.

Interpreting these dates in a linear arrangement, it would seem that transformation proceeds in a wave downstream, being earliest at Yellowstone Lake and progressively later at points farther down. In how far these dates accord with those of other years is problematical. According to Mr. A. G. Whitney, in 1922 recession of water occurred earlier and the stoneflies appeared about two weeks earlier than in the preceding year.

Transformation takes place early in the day, within the first four hours after sunrise, the greatest number emerging at about eight o'clock. Stragglers continue to emerge practically all morning—indeed, occasional specimens were observed transforming in the afternoon. For ecdysis the nymphs climb up any convenient point along the shore—into grass, onto stones, brush, trees, etc. (Figs. 100 and 102). On the whole, they prefer open places along the stream. Also, the slack waters of eddies are sought. In rapids, the various emergent rocks, and in smooth stretches some mid-stream boulder, form convenient places for emergence. Ecdysis then takes place on the shaded side of any object to which the nymph has anchored itself by means of its legs.

Fig. 79. Hot spring on shore of Yellowstone River, covered in June. Aug. 15, 1921.

Fig. 80. Cleft boulder on meadow between Yellowstone and Lamar rivers. June 17, 1921.

Fig. 81. Brink of Lost Creek Canyon to right, and "crater" in foreground. The meadows are said to be the bottom of the crater, the hills around forming the rim of an extinct volcano. Aug. 28. 1921.

Fig. 82. Castle Rock (also called Cathedral Rock) on North Fork of Clearwater River, Idaho. Showing types of shores and placid stretches of stream. Sept. 2, 1924.

The slow pumping action and inflation to split the nymphal skin can be readily observed. Eventually the skin splits on the dorsal side on a line between the wing pads and the occiput, the thorax pushes up and through the slit, the feet are partly withdrawn, then the head, the entire thorax and legs, and finally the abdomen. The whole process may take from twenty minutes to an hour.

Spreading of the wings then proceeds, during which process the adults generally cling to their exuviae. The adults take flight in a very few minutes, while the wings are still very soft and pliable. They fly to some higher object near the stream, generally to some tall bush or small tree; and if a person be in the vicinity, he too may serve as an alighting place and shortly may be covered with these fluttering insects. Observation indicates that the points sought are such as give suitable exposure to the light and to the breezes for the purpose of drying their wings; direct sunlight is never sought. The adults spread and move their wings freely during this process. In addition, they exude yellow or salmon-colored droplets from the anus, which may be blood or merely waste products, it is unknown which.

Copulation in this species takes place late in the day, oviposition apparently at any time in the day. For oviposition the female descends on rocks to the water surface and dips her abdomen into the water and permits the eggs to be washed off in the lesser currents along the shore.

A curious phenomenon noted for this species and for *Acroneuria pacifica* is the crepuscular flight upstream. This begins immediately after sundown and lasts till after dark. Swarms of thousands of specimens take flight, hovering from 50 to 200 feet above the water, depending somewhat on the height of the shores. Since both sexes participate in this flight, it might be regarded as a "nuptial flight." But, as already noted, copulation does not take place during flight, but when the specimens alight in tall grass, low trees, and bushes, or lacking these, in crevices of rocks, or grooves in the sand. It is therefore not at all clear how this flight is to be interpreted. Practically, however, the instinct serves effectively to repopulate the headwaters of the various streams. During the upstream flights numberless thousands are caught in the vortices, back drafts, and wayward air currents, and are hurled to the stream beneath, where they eventually form an important item of the surface food of trout.

Adult life normally lasts but three to four days. Relatively few specimens die a natural death. Being awkward fliers, during their short flights they are readily swept into the water by wayward air currents. Others form juicy tidbits for hundreds of birds. Still others may be eaten by small mammals. In the morning one finds hundreds of severed wings along the shores of the stream, indicating perhaps the active feeding of the birds during the early hours. One morning, at a point near the Cooke City bridge, in a gravelly depression about three feet in diameter, I counted the wings of over 200 *P. californica* and *A. pacifica*. Most of these I removed. Next morning an approximately equal number of detached wings lay in the same depression. I was unable to tell whether mammal or bird or other creature had feasted there.

Pteronarcys californica is primarily a river species, abundant only in the larger mountain streams, and rather scarce in the precipitous creeks. It is found throughout the Northwest.

Acroneuria pacifica, which is very closely associated with *P. californica*, was even more abundant. In the main, what has been said about the larger species applies also to *A. pacifica*, with the exception that the nymphs are quite squat and smaller, and that they are much more active. On shore the adults also seem to be more active than the larger species (Figs. 101 and 102).

For July 21 I have the following note: "Yellowstone River shores strewn with wings of *P. californica* and *A. pacifica*. Many caught in spider webs with Tipulids and caddisflies. Many others water-trapped. Eaten by birds (nighthawk, robin, etc.). Also snakes (garter snake) here that feed on the adults. Ground squirrels seen twice feeding on *Pteronarcys* adults."

Garter snakes were seen on various occasions feeding on stoneflies. July 15 six garter snakes were observed feeding on these insects in the stone rubble that marks the Elk Creek eddy of the Yellowstone. On July 16 some twenty garter snakes were noted along the Lamar, most of them feeding on the stoneflies. A frog taken along the Lamar and examined for the stomach contents showed several adult *Acroneuria*, a beetle, and some diptera.

Of other species, *Acroneuria theodora* deserves mention. Its emergence occurred early in August along the Gardiner and Lamar rivers. Very few adults were seen and none of the nymphs, except for some exuviae. This is not a common species.

The smaller species of stoneflies, with adults of pale greenish or yellowish hue, are somewhat inconspicuous because of their small size. One finds the nymphs most frequently among the rocks on the bottom of midstream pools, and very sparingly among the rocks of rapids. Their food is chiefly animal matter. Their emergence seems more prolonged, and not confined to a relatively short period like that of the larger species. On the whole, the smaller species are much more abundant in smaller creeks and along the shores of mountain lakes than in the larger streams.

INSECTA. *Ephemeroidea*.—Of the mayflies the following have been identified: *Ameletus* sp., *Callibaetis* sp., *Drunella grandis*, *Ephemerella coloradensis*, *Ephemerella* sp., *Heptagenia* sp., *Iron longimanus*. This list is rather fragmentary, since most of the species were available only in nymphal form. An attempt to breed the nymphs has already been mentioned; to the persistence of the bears in wrecking my arrangements may be ascribed the lack of more specific identifications.

Two types of habitus are present among the nymphs, the swimming and the clinging. Thus, one encounters the cylindrical and slender nymphs as typified by *Baetis* and *Callibaetis*, and the flat appressed type of *Heptagenia*, *Iron* and other forms.

The food, as indicated by examination of the stomach contents, is largely offal. The food average for 25 *Ameletus* nymphs was: plant food 22.7%, detritus 77.3%; for twenty *Drunella*, 18.6% animal food, 36.8% plant food, and 44.7% detritus; for two *Baetis*, 50% plant, and 50% animal food; for 28 *Ephemerella*, 3.6% animal, 36.3% plant food, and 60% detritus; and for 34 *Heptagenia*, 24% plant food and 76% detritus.

Some of the *Drunella* nymphs were heavily infested with *Gregarina*. On the other hand, two *Heptagenia* nymphs were found to be parasitized by a nematode parasite (*Mermis* sp.). Figure 103 shows an adult mayfly with such a parasite emerging. The specimen was taken at the entry of Lava Creek into Gardiner River; it was fluttering weakly and the weight of the parasite held it from rising above the shallow rapids at that point.

Transformation for all species was very irregular and seemingly strung out during the whole summer. One could expect to find a few adults transforming every day. No attempt was made to secure a series of adults. This was mainly for a personal or selfish reason. Usually laden with bottles, water nets, cameras, luncheon, etc., an extra net and cyanide bottles might be more of a load than would be comfortable for a tramp of many miles.

INSECTA. *Odonata.*—Relatively few dragonfly species are known from rapid streams, and even fewer from mountain streams. Only a single species, an *Ophiogomphus* (probably *montanus* Selys), was found, of which three adult females and some eight or ten exuviae were collected. Strange to say, all of these were found in one locality, some fifty yards below the Cooke City bridge across the Yellowstone. On July 30 the emergence of a specimen was observed in detail. The following is taken from my field notes of that date:

"10:37 a.m.—Gomphid climbed out of water. Immediate shore here is somewhat sandy. Climbed onto rock.

10:45—Thorax split open.

10:46.5—Head and thorax thrust forth.

10:50—Head, thorax, and legs out.

10:58—Abdomen out to 4th segment, wings elongating.

11:02—Abdomen out completely.

11:05—Wings unfolded to one-half their adult length. Abdomen shows no change.

11:12—Wings open to stigma.

11:14—Wings open to tip, now ⅓ longer than abdomen.

11:15—Abdomen beginning to be inflated, insect clawing for hold on rocks and exuviae.

11:17—Insect leaves skin for hold on rock.

11:18—Pumps abdomen with visible effort, swaying from one side to other.

11:20—Abdomen extends to beginning of stigma on wings. The wings are folded roof fashion to side of abdomen, which is pressed firmly against them, to aid in process of inflation.

11:21—Abdomen extends to end of stigma.

11:21.5—Droplet forms at end of abdomen and drops into water.

11:22—A second droplet.

11:22.3—Third droplet.

11:22.4—Fourth droplet.

11:22.5—Fifth droplet.

11:22.8—Sixth and seventh droplets.

11:23—Eighth droplet.

11:23.5—Ninth droplet. Abdomen reaches to tip of hind wings.

11:24—Three droplets in rapid succession.

11:25.2—Two more droplets. No more fell after this.

11:28—Abdomen extends slightly beyond tips of hind wings.

11:30—Abdomen ¼ in. beyond tip of wing.

11:45—Abdomen deflated.

11:50—Leaves for top of rock and extends wings for flight. Captured on 'take off.' "

Two other females were captured the same day. Specimens of this species were also seen on the following days along the Gardiner and Lamar rivers, but were not captured.

In the neighborhood of mountain streams one frequently sees specimens of *Sympetrum*, *Aeschna*, *Lestes*, *Enallagma* and other pond forms. These come from nearby quiet waters, or, as in the case of Lost Creek, may even occur in beaver ponds; that is, in such ponds as result from damming of the flow of the creek by the beavers. The fauna of these ponds is of a mosaic type, as a rule, consisting of a very few representatives of pond life.

Insecta. *Hemiptera*.—The aquatic bugs are hardly endemic to mountain streams. Like many other aquatic insects, they may occasionally be found in marginal pools, ponds, and in swamps and springs. Thus, *Notonecta* may be found on rare occasions and with it *Corixa*, and more frequently some water strider or surface skimmer. In Yellowstone Park I encountered water striders on the Lamar, Tower Creek, Lost Creek, and Gardiner River; invariably they marked the neighborhood of some spring-fed pool or clear pond. In Idaho I have seen the skimmers along the Snake, St. Joe, Clearwater, Elk, and Oro Grande rivers, in Glacier Park along MacDonald Creek, Two Medicine River, St. Mary's River, etc. There, too, they seemed to be migrating from some neighboring pools.

Insecta. *Trichoptera*.—Only generic identification was possible for most of the species taken, due to lack of adult stages. For here, too, the bears interfered. For breeding cages I had used some of the familiar cone-like fly traps of wire, which were fitted over stones harboring various caddisworms. These the bears were not satisfied to tip over, but removed them completely; I did not discover what they did with the traps. Following are the species determined: *Brachycentrus* sp., *Glossosoma* sp., *Goera* sp., *Hydropsyche scalaris* Hagen, *Hydropsyche* sp., *Limnophilus* sp. (near *rhombicus* L.), *Molanna* sp., *Neophylax concinnus* Hagen, *Philopotamus* sp., *Platyphylax* sp., *Rhyacophila coloradensis* Banks, *R. fuscula* Hagen, *R. torva* Hagen, *R.* sp., *Thremma* sp., *Triaenodes* sp.

Of these species the four most conspicuous are *Hydropsyche*, *R. torva*, *Brachycentrus* sp. and *Thremma* sp. Of these the first is a web-spinner, the following two have fixed cases, and the last a movable case (except during the pupal stage, when the case is fastened). In the creeks *Thremma* and *Hydropsyche* seemed abundant, in Yellowstone River the other two species. *Hydropsyche*, strictly speaking, is of wider distribution than other species of the mountain waters.

Fig. 83. Clearwater River, Idaho. Showing sand deposits left by spring flood, and log jam in river. Aug. 31, 1924.

Fig. 84. Clearwater River, Idaho. A closer view of log jam caused by spring flood. Also showing "The Gates" and government bridge across river. Aug. 31, 1924.

Fig. 85. Hibernating Coccinellidae. Photograph taken on a warm spring day when sun brought out the beetles. Many had been washed into a creek about twenty feet away. Photograph Moscow Mt., Idaho, about April 15, 1923.

Fig. 86. Skeleton of winter-killed buffalo, near Lamar River eddy. Note the puparia of flies on the scapula. The skull had been dragged into the eddy by some animal (bear?). July 25, 1921.

The fixity of the cases results in an enormous death rate for *Brachycentrus* and *Rhyacophila*. During the high water period their cases are attached to rocks that are then submerged; with the quick recession of waters these cases are "stranded" and their inhabitants die within them (Fig. 104). On several occasions a number of these stranded cases were opened to see if the larvae had left them in order to build new habitations. The stranded cases contained dead larvae and pupae. Very quickly these form the food for scavenging shore forms, such as Staphylinidae, a *Silpha*, Carabidae, and ants of various kinds. This "death by stranding" was most notable along the Lamar River, where the recession of water was very rapid.

For *Brachycentrus* two methods of attaching the square cases were noted. One was to attach them by the base, i. e., the small end, so that the cases stuck out from the rocks at right angles (Figs. 104 and 105). The second was an attachment by means of a "lip" at the wide or head end of the case; usually this occurred close to the surface so that the surface layer of water would sweep directly into the case. When a stone carrying such cases was lifted above the water surface or to a point where the water did not completely cover the opening, the larvae would pull the case to an oblique or right angle to the rock, bite off the secretion attaching the case and then crawl down the rock to a point where the current was suitable. The cases were submerged from one-fourth of an inch to six inches in fairly strong rapids.

Empty cases of *Brachycentrus* seem to afford opportunity for the development of a micro-fauna of their own, particularly of Protozoa, Rotifera, and an occasional Hydrachnid.

The food of caddisworms is quite generalized. Thus, 32 *Rhyacophila* contained 49% animal food, 23% plant food, and 28% detritus; 27 *Hydropsyche* had eaten 42% animal food, 54.3% plant food, and 3.7% detritus; 33 *Brachycentrus* consumed 18.3% animal food, 72.7% plant food, and 9% detritus; and 23 *Thremma* included 28% animal food, 64% plant food, and 36% detritus in their diet. On the whole, the first three take their food as it comes to them, while *Thremma* selects what food it consumes. All of the forms are cannibals on occasion (see Muttkowski-Smith).

Connected with the feeding one may note the extent to which the various species are parasitized—*Rhyacophila* with *Gregarina* in about 40% of the specimens examined, *Hydropsyche* about 60%, and *Brachycentrus* fully 100%. None of the specimens of *Thremma* contained any parasites. This is possibly correlated with the fact that their food was primarily selected, while the other forms ate what food was swept along with the flotsam down the stream. Much of this flotsam consists of crushed and torn specimens of insects.

The adults have the habit of flying above rapids, running up the wet rocks, and also dipping into the water. This habit exposes them to capture by fish; indeed, they were numerous among the stomach contents of trout. One trout was found to have gorged itself with caddisflies, the total number exceeding 500 specimens.

Insecta. *Diptera*.—Only three families can be said to be typical in mountain streams. These are the Blepharoceridae and Deuterophlebiidae, or net-

winged midges, and the Simuliidae or Buffalo gnats. Besides these, isolated genera of Chironomidae, Leptidae, Tipulidae, and Psychodidae breed in rapid streams. In addition, the adults of some species must be listed as hovering near swift water, chiefly on rocks that are sprayed by the stream.

The most typical residents of swift streams are the Blepharoceridae. This family was represented by two species, *Bibiocephala comstocki* and *B. grandis.* Where the current is swiftest, where their abiding places are perhaps the most inaccessible, there one is likely to find the larvae of these species. Their presence was first noted on the Lamar River, on June 23, when several dead larvae were found stranded in a flood pool. Somewhat later, June 28, stranded pupae were noted. The first adults were seen July 5, on the rocks in Yellowstone River, "on the shady side of the large boulders in the strongest current, gathered in groups of forty or more. Very difficult to secure with a net (dip-net). Some drop into the water, and appear to have little difficulty in reaching a rock again. Apparently somewhat hydrofuge (notes of July 5)." The adults were found from July 5 through the following months. The last were observed September 6 (into October in Idaho streams). Pupae were found quite frequently during the low water stages, but the larvae only very rarely (Figs. 106, 107 and 108).

Because of their very firm means and methods of attachment one would hardly expect to find the larvae and pupae in fish stomachs. Yet they do occur in trout food. The adults occur much more frequently among food items of fish than do the earlier stages.

One of the most noteworthy discoveries of the summer was that of a *Deuterophlebia* larva (Fig. 109) in Yellowstone River on July 30. This enigmatic larva for several years defied any attempt at identification. Very recently its identity was established, through the courteous aid of Dr. Johannsen of Cornell University. A detailed account of this new American record has been published elsewhere (See Bull. Brooklyn Ent. Soc., Vol. 22, pp. 245-249, 1927).

Deuterophlebia was described from a pair of male specimens from India, which formed the type of a new species, genus and family of Diptera. Several years later the larval stages were described by Miss Pulikovsky from materials received from the Altai Mountains in Siberia. The Yellowstone River larva establishes this genus and family for North America. For the Park there are three records:

July 10. Lost Creek at Camp Roosevelt. Pupae taken from sluice-dam. Elevation about 6300 feet.

July 30. Yellowstone River, at Cooke City bridge. One larva caught in plankton net. Elevation 5900 feet.

Aug. 2. Tower Creek Canyon, about four miles above Tower Fall. Pupae taken from rocks holding *Bibiocephala* pupae. Elevation about 6700 feet.

While the pupae of both families are very similar, the larvae are very unlike, as will be seen upon comparison of the figures 106 and 109. *Bibiocephala* is long and flat, with a series of ventral suckers; its locomotion is extremely slow and clumsy. *Deuterophlebia* has a number of pro-legs with terminal pads for attachment; although the locomotion was not observed, to my

mind the pro-legs operate much like the tube-feet of Echinodermata. The similarity of the pupae is regarded by Miss Pulikovsky not as indicating relationship, but as a clear case of convergence, similar to that shown by certain Psychodidae. No adults were taken in Yellowstone Park. But I suspect from the similarity of habitats and from what Miss Pulikovsky has written that the adults probably show similar habits.

The larvae of Blepharoceridae (and Deuterophlebiidae) are found where the conditions of mountain streams are most strenuous, namely, in the strongest rapids and behind water-falls. The pupae are found under similar conditions. The adults like to sit on rocks, near the surface of the water, where the spray keeps the rock continually moistened.

The third family of Diptera that is confined to rapid waters is the family Simuliidae. It is very probable that a number of species are represented in the streams of Yellowstone Park. Of the fifty-five blackfly species of North America listed by Dyar and Shannon ('27), some eighteen are regional; that is, they occur in regions adjacent to Yellowstone Park. In fact, seven of these regional species were actually taken in the Park, chiefly at Mammoth Hot Springs and Old Faithful. It is very likely therefore that the specimens collected and observed in the various streams represent more than one species.

In the Yellowstone the larvae and pupae were quite scarce after the spring flood, and none too frequent in the Lamar. At the same time the small tributary creeks and rills contained an abundance of *Simulium* From observations made during the summer it seems that the larger streams are restocked every year by specimens from the smaller tributaries. Thus, at the mouth of Elk Creek, on July 15, the stones were covered with large patches of *Simulium,* while the Yellowstone showed none of these larvae. About three weeks later the river, too, showed an abundance of *Simulium* just below the mouth of Elk Creek. Similarly in Lost Creek at the time of high water (about June 20) *Simulium* was very scarce. On June 19 a small rill leading from the creek to the meathouse of Camp Roosevelt was found heavily infested with *Simulium* larvae and pupae. Lost Creek above and below the rill showed few traces of the species. Turning the water from the rill for two days dried up the *Simulium* and stopped their appearance at the camp during the summer. As the waters of Lost Creek fell, *Simulium* became more and more abundant and conspicuous.

In Yellowstone River the larvae were found to contain a considerable portion of lake plankton in their food. This was evidently swept downstream from Yellowstone Lake, and the larvae combed this food from the waters (Fig. 110). In turn the larvae and pupae are eaten by fish. Small *Pteronarcys* nymphs were observed feeding on them; it is also probable that at least *Hydropsyche* among Trichoptera and the larger mayfly nymphs feed on *Simulium.*

A nematode parasite is quite frequent in the larvae. A field note of August 11 is pertinent: "Yellowstone River. *Simulium* was found extensively parasitized. Certain individuals were noted with swollen caudal end and of greater length than others. These specimens were invariably pale green on their venter. A green *Mermis* (?) was noticed in the net. Comparison elicited the fact that all swollen individuals were parasitized. It was not determined whether any

pupae were parasitized or if parasitized individuals could pupate. It was evident that the *Mermis* were leaving the larvae for their free-living adult stage. Just at what point they left the *Simulium* was not established. It was noted, however, that the parasite was coiled chiefly at the posterior end of the larva, with a small coil near the head."

Of families with occasional representatives in mountain streams, the Psychodidae, Chironomidae, and Leptidae should be noted. A species of *Psychoda* was caught quite freely along the various streams, but none of the larvae were found. It is probable, according to Thienemann, that the larvae would be found among the deposits on rocks.

Of Chironomidae the following species were found: *Ceratopogon* sp., *Chironomus* sp., *Cricotopus varipes*, *Metriocnemius* sp., *Orthocladius* sp., *Procladius* sp., *Tanytarsus exiguus*. It is probable that many more species are represented; but since the main attention had to be given to the more dominant and conspicuous forms, the chironomid collections were perforce somewhat neglected. *Ceratopogon* larvae were found repeatedly in the sandy spots in Lost Creek, among the accumulations between rocks, and in the marginal areas. No pupae were obtained. *Cricotopus* and *Tanytarsus* were conspicuous in the sulphur and slime deposits on rocks along the shores and in midstream on submerged rocks. There they gathered and built their tubes by the thousands into a flocculent mat, among which rock diatoms and algae thrived. Here, too, might be found the Vorticellidae (*Hydra* also, in European streams). Young fish fed on these mats with eagerness; but larger fish seemed to despise them and came to them only when extremely hungry.

Adult midges could be seen flying along the shores among the grasses or into the spray of the lesser and shallower rapids.

The Leptidae are represented by *Atherix variegata* Walker. The larvae have a rather wide distribution in mountain streams and are frequently found in trout stomachs. For the adults, Malloch's account can be quoted (p. 363): "The females of the genus Atherix have a peculiar egg-laying habit. The eggs are deposited upon branches or twigs of willows or other trees overhanging streams. After oviposition the female does not fly away, but dies and remains attached to her egg-mass. The second female adds to the already deposited mass both her eggs and her body, and gradually others do likewise, until the combined mass of eggs and flies assumes considerable proportions, often containing several thousand dead flies. The larvae which hatch drop from the mass into the stream below, where they pass the immature stages. The Indians in Oregon at one time collected the masses of eggs and flies and used them as food. An interesting account of this aboriginal utilization of nature's resources is given by Prof. J. M. Aldrich (Ent. News, Vol. 23, pp. 159–164)."

The cluster shown in figure 111 measured about seven by twelve inches and was fastened to the underside of an overhanging rock. The position of the rocks is indicated in figures 71 and 112: figure 65 shows the same rocks from the distance. The photograph was taken under somewhat difficult conditions, since at the time the base of the rock was surrounded by rapids. My notes for that day are as follows: "Flies in cluster arranged in shingle fashion, each

Fig. 87. Huge boulder in stream bed of Oro Grande River, Idaho. This boulder is fully forty feet high. Smaller boulders can be seen on the slope along the river. Sept. 2, 1924.

Fig. 88. Trick Falls, Glacier Park, in Two Medicine River, a short distance below Middle Two Medicine Lake. Photograph July 17, 1925. The Same place was visited Aug. 26; the lower part of the falls, which emerges from an underground conduit, was then completely dry.

Fig. 89. Keppler Cascade, Yellowstone Park. Aug. 18, 1921.

Fig. 90. Oro Grande River, Idaho. Freak roots of a tree on top of a boulder. One root circles to the left and then turns under the tree. The boulder is surrounded by water, and none of the roots passes into the stream bed; the boulder showed no sign of being cleft.

straddling neighbor in part. All so arranged that at periphery of cluster the individuals face outward. Unevenness of rock has caused several whorls. Composed of thousands of specimens. All dead. These are this year's flies. Cause of death unknown. Came here for oviposition, for under them a fibrous deposit is full of eggs, some of which are hatching. The mass is invaded by a number of *Trox* adults, and *Dermestes,* also one or two Staphylinids." My last notation is of August 23: "Winds and scavengers have stripped the patch so that only very few dead *Atherix* remain. But *Dermestes* larvae are still feeding on them."

The Tipulidae, too, seem to be represented, for along the shores in the moist sand or earth, between rocks, or submerged, one finds tipulid larvae of various types. No attempt was made to collect them systematically, since they appeared to be rather infrequent. One peculiar larva collected is shown in figure 113, taken from Tower Creek, August 29. This larva inflated its posterior end in balloon fashion; for what purpose, is not known.

Diptera are further represented by what I have called "splash flies" or "spray" flies. These are the adults of *Philolutra simplex* and *Chamaedipsis comata* Melander. They occur in fair numbers on the exposed rocks of streams (Figs. 93 and 114). They make short flights to the water surface, alight at the immediate edge of the current on the rock, and then run upward through the spray. They seem to prefer the shady side of the rocks. Quite generally they were mixed with *Bibiocephala.* Like these, I found them during the entire summer, and even later in Idaho streams. The earlier stages are unknown to me. Whether they are native forms or merely visitors I was unable to ascertain. They are much more numerous than the Blepharoceridae, but despite this they are much less frequent in fish stomachs.

Among casual visitors near the water, *Boletina melencolica, Mycomyia mendax, Linanculus querulus, Leptocera* sp., *Paralimna* sp., *Empid* sp., have been identified. It is very probable that many of these breed under moist conditions, hence not in the water, but at the margins of streams.

INSECTA. *Coleoptera.*—The bettles like so many other aquatic types, are practically absent from the mountain streams of the Park. Certain species (*Hydrobius scabrosus* Horn, *Agabus tristis* Aubé, *Crenitis monticola* Horn, *Deronectes griseostriatus* DeGeer, and *Hydroporus* sp.) were found in the marginal shallows and pools, especially in the recession pools. The test for the true fauna of the mountain streams lies in the food contents of fish stomachs. Endemic species will be found there in the larval and adult form. Surface drift can be readily distinguished. Thus, the beetles noted above are practically entirely absent from the stomach contents either as larvae or adults. In fact, one finds them *only* as adults, if present at all. If one wishes to find the larvae of these species one must look to the ponds and small lakes and marshes.

What surprised me was that the streams did not show any Parnidae and Dryopidae (Figs. 105 and 106), the typical beetles of lake shores. Idaho streams such as the Clearwater, the Palouse River and others, in places show an abundance of *Psephenus* larvae and occasionally other parnid species. But in Yellowstone Park they seem to be quite rare. I have one record of a *Psephenus* skin, August 11, Yellowstone River, at Cooke City bridge, "taken from *Simu-*

lium society." This may have been carried down from Yellowstone Lake. Another record was "June 28—Parnid larva taken from Lost Creek." This was placed in a screened jar with the hope of breeding the specimen. With this jar were a number of others, containing various stonefly nymphs, mayfly nymphs, and Trichoptera larvae. Unfortunately, as already noted, the bears of that region had too keen a scientific curiosity and wrecked my breeding arrangements by tipping over the jars, scattering them downstream or removing them altogether.

Shore beetles of various sorts play the parts of scavengers on various stranded biota (*Cicindela, Dermestes,* Staphylinidae; see notation under Trichoptera). Another situation was of considerable interest. This was in connection with the *Atherix* cluster described (see Diptera). Although the cluster could hardly have been more than a week old at the time of its discovery, still the larvae and adults of *Dermestes talpinus* Mann. and the adults of *Trox* sp. and several forms of Staphylinidae were feeding on the dead *Atherix* adults and on the developing eggs.

c. *Chordata.* Practically all the classes of Chordata are represented in the mountain waters and affect its biota either directly or indirectly.

1. Fish.—The characteristic fish of the mountain streams are the native red-throat trout (*Salmo clarkii*), which are found in the highest elevations. Besides these one may also find minnows, occasional bass, suckers, pea-mouth, bullheads, *Cottus,* and graylings. *Cottus* has been found at surprisingly high elevations: *Cottus punctulatus* (Gill) is recorded from the Yellowstone, and other species from various rivers of the Northwest. The grayling (*Thymallus*) is held by Thienemann as typical of the lower elevations (below 1000 meters) of rapid streams. In Idaho streams I have found *Cottus,* bullheads, pea-mouths, and other fish at elevations of 3000 feet and less, in the larger streams.

In Yellowstone National Park (and to a lesser extent in Glacier National Park) the planting of exotics (non-native fish) in the lakes and streams, including various foreign trout, whitefish, pike, pickerel, rock bass, silver bass, perch, etc., has perhaps affected some of the faunal complex, at least of the lakes. Records of plantings are not available except for recent years. In places it is therefore difficult to tell whether the fish present are native or foreign. On the Pacific slopes the upstream migration of the salmon annually affects the headwaters of streams. No food is eaten by the salmon, but the spawning and the ensuing death, followed by decay of the adults, probably affects the life and physiology of the stream in many ways. This is a problem that invites study.

2. Amphibia.—No amphibia are native to the mountain streams. Frogs and in one case a salamander or newt (not captured) were found at points where ponds, and marshes occur. Generally the frogs are only visitors to the streams, or may have wandered away from their proper habitat.

On rare occasions one may find frogs among the stomach contents of fish. I have only one record of a frog taken as food by trout, in the meadows of Slough Creek. As a matter of fact, several attempts were made to use small frogs as bait for trout; the fish seemed uninterested and refused it. In turn the frogs eat much of the insect life along the streams—stoneflies, caddisflies, beetles,

Fig. 91. MacDonald Creek, Glacier Park. Just above the falls the stream bed consists of stratified rock. Aug. 17, 1925.

Fig. 92. Yellowstone River, at Cooke City bridge. Showing rapids and marginal pools. Aug. 15, 1921.

Fig. 93. Yellowstone River showing rocks with "splash flies." July 7, 1921.

Fig. 94. Lamar River eddy, showing marginal pools. Later these pools became dry. Pool at upper left is completely cut off from stream. In the middle the moist bottom of a recession pool shows clearly. July 16, 1921.

etc. The stomach contents of a frog taken along the Lamar showed several *Acroneuria pacifica,* some beetles and flies.

3. Reptilia.—Snakes are frequent visitors along the shores of mountain streams. Garter snakes were noted repeatedly—six on one day, over twenty on another—feeding on whatever food good fortune might cast their way. Preferably they would feed in places where rocks were heaped, or where such rocks were sufficiently close and with spaces between and under them to provide proper shelter and good hunting ground. Repeatedly I observed the garter snakes catching and eating adult stoneflies (*Pteronarcys, Acroneuria*).

In no way connected with the work was the capture of a "rubber boa" on the evening of August 10, along the road between Tower Fall Junction and Tower Fall. Dr. C. C. Adams and Dr. G. M. Smith were with me at the time. The specimen was sluggish in behavior, very inactive and rather docile when picked up. It was later identified as *Charina bottae* (Blainv.). This species is widely distributed along the Pacific Coast. Since then I have seen it in Idaho, near Moscow Mountain; and from descriptions of students, farmers, hunters, etc., I find that it occurs throughout Idaho and western Montana.

4. Aves.—Of birds only one can be called a species of the mountain streams, the water ousel or dipper (*Cinclus mexicanus unicolor*). This is the characteristic bird of the rapids. There one may observe it on exposed rocks, "dipping" in characteristic fashion. From time to time it wanders into the water, through the rapids, disappearing completely beneath the surface in search of food. Frequently it emerges some twenty-five or more feet away from the point of entry.

Along the shores nighthawks (*Chordeiles virginianus hesperis*) robins (*Planesticus migratorius propinquus*), and other birds were seen feeding on stoneflies. Thus, morning after morning during early July one might find hundreds of stonefly wings (of *Pteronarcys* and *Acroneuria*) gathered in some favorable spot, apparently stripped from the insects before they were eaten. Although nocturnal observation was difficult, I feel certain that quite a number of birds followed the crepuscular flight of the stoneflies and fed on the swarms (see stoneflies, p. 189).

5. Mammalia.—Visiting mammals are not at all infrequent along the mountain streams. Most noteworthy are the moose (*Alces americanus shirasi* Nelson), the elk (*Cervus canadensis canadensis* Erxleben), mule deer (*Odocoileus hemionus hemionus* Rafinesque), White-tail Deer (*Odocoileus virginianus macrourus* Rafinesque), various mice, beavers (*Castor canadensis canadensis* Kuhl), otters (*Lutra canadensis canadensis* Schreber), black or cinnamon bears (*Ursus americanus* Pallas), and water shrews (*Neosorex palustris navigator* Baird).

Of these the beavers, water shrews, and otters can be said to affect the stream life directly, the others more or less indirectly. The bears were constantly noted along Lost Creek, and Lamar River, plunging in for a bath, fording the stream, or perhaps looking for some toothsome fish. Water shrews were observed only twice, swimming about actively in search of aquatic insects. The beavers affect the smaller streams primarily by damming. The domiciles and engineering feats of beavers may be observed at thousands of points along the streams of the Northwest. Lost Creek, Carnelian Creek, Lava Creek, etc. are

excellent illustrations of dammed streams. Along Tower Creek there are a considerable number of large springs which have furnished sites for a number of beaver works.

The results of such damming of streams are both direct and indirect. As direct results may be indicated the destruction of current for long stretches and hence a modification of the streambed and of the constitutive fauna and flora. An indirect result is the drowning of adjacent forests, which in time leads to the alteration of the stream banks.

ECOLOGY OF MOUNTAIN TROUT STREAMS

A. General. In the first part of this paper four types of mountain streams were distinguished: the constant streams, the flood or variable streams, the precipitous streams, and the temporary hillside streams. This classification does not agree with that of Steinmann ('07) for the alpine streams of Switzerland. Steinmann recognized two types of mountain streams, (a) the elevated mountain streams (Hochgebirgsbäche), which have their origin from the melted snows of elevated fields and mountain sides and from glaciers; (b) middle mountain streams (Mittelgebirgsbäche), which are fed by springs. The latter might also be called valley streams since they traverse the mountain valleys and there gather the waters of tributaries.

Thienemann ('12) notes certain weaknesses in this classification, notably the fact that it is based on altitude, and that insufficient distinction is made between the major habitats and their subdivisions. Based on the study of streams of the lower mountains of Germany, Thienemann adds certain elements and offers the following classification:

A. The springs and their outlets, which are fishless.
B. The elevated and middle streams, which contain trout.
C. The lower streams, which contain grayling.

Springs and rills solely would be found in the higher altitudes. These are followed by streams which contain Salmonidae; these in turn by streams in which the Cyprinidae predominate.

Both Steinmann and Thienemann consider the spring biota as ecologically related to those of the mountain streams. While granting a physiographical continuity between spring outlets and streams, an ecological continuity appears to me to exist only under exceptional conditions. In no place does this become so apparent as in Yellowstone Park. Although in the present study the springs received little attention, a word about them may not be amiss. After a number of reconnaissances of the aquatic conditions in Yellowstone Park I recognized the futility of obtaining even to a slight extent a fair picture of the true relations of the springs to streams. For the springs of the Park are not only multitudinous in number, but also multitudinous in variety One could employ a dozen different criteria for their classification and still not exhaust them. One might classify springs according to topography, whether their waters immediately fall away after leaving the ground or whether they are caught in a pool of varying size (Bornhauser). One could also classify them according to size and temperature; as for the latter, the springs range from icy chilliness to boiling point. One might arrange

Fig. 95. Yellowstone River, rapids and whirlpool, a short distance above Cooke City bridge. July 7, 1921.

Fig. 96. Lost Creek, showing tangles and underbrush along stream. Sept. 2, 1921.

Fig. 97. Spider webs, with prey of aquatic insects. From rocks beside Lost Creek Falls. Sept. 2, 1921.

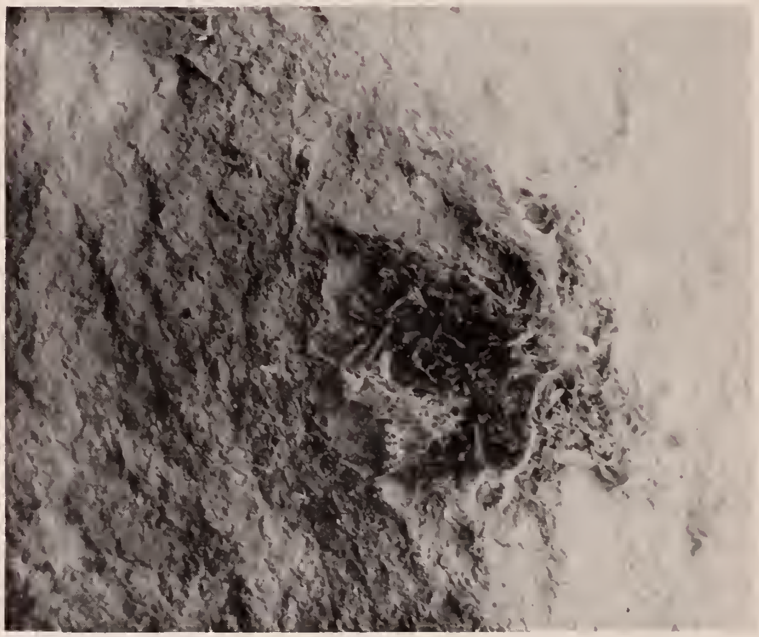

Fig. 98. Detail of a spider web, showing various insect adults. Lost Creek Falls. Sept. 2, 1921.

them according to color, which not only differs among different springs, but often in the same spring at different times. Again, one could classify them according to substances in solution, such as carbonates, arsenates, chlorides, silicates, sulphides, etc.; or according to substances in suspension, such as sulphur, mud, sand, silt, etc. In fact, every conceivable type of spring occurs in Yellowstone Park and feeds the various streams (see Brues, '24).

In the main, the influence of these springs is only a local one, that is, circumscribed and limited to a very small area of influence, although at least in the Firehole River in the Upper Geyser Basin the temperature and chemical composition of geysers and springs modify the river water sufficiently to affect the faunal makeup. But all these various factors modify the composition of the spring biota and of the plants and animals found in their outlets.

It was the realization of the great variegation of the springs that quickly dissuaded me from attempting to study in detail the relation of the fonticolar to the torrenticolar associations. The excellent studies of the fauna of thermal springs in Yellowstone Park made by Brues in 1923 indicate many of these difficulties of ascertaining this relationship.

B. Classification of Habitats. Even at first glance it is evident that mountain streams, with their major and minor falls, their many winding and tortuous rapids and channels, their indescribable intermingling of tumbled and placid waters, represent a highly specialized habitat, indeed, the pinnacle of aquatic specialization, comparable only with shores of oceans and larger lakes. Yet it is also obvious that this biotic unit is composed of simpler associations, each with its individual peculiarities. A classification of these must necessarily be based partly along physiographical, partly along physiological lines. Thienemann ('12) offers a classification, with which, as indicated in part II of this paper, I am unable to agree. For the sake of clarity the two groupings are here placed side by side:

AFTER THIENEMANN.

- A. Types of streams.
  - 1. Rills and Springs.
  - 2. Streams.
    - a. Elevated streams and middle streams, trout streams.
    - b. Lower streams, grayling streams.
- B. Ecological Habitats.
  - 1. Springs and rills.
  - 2. Stream.
    - a. Open water.
    - b. Bottoms and surface.
      - aa. Stone fauna.
      - bb. Plant fauna.
      - cc. Quiet inlets and bays.
        - —on the water.
        - —among leaves and dead branches.
        - —in sand and mud deposits (slimes).

AUTHOR'S CLASSIFICATION.

- A. Types of Streams.
  - 1. Rills and Springs.
  - 2. Streams.
    - a. Constant.
    - b. Variable or flood.
    - c. Precipitous.
    - d. Temporary. (Springs and rills)
- B. Ecological Habitats
  - 1. Permanent habitats, with native biota.
    - a. White water habitats — falls, cascades, white rapids.
    - b. Clear rapids and stone bottoms.
    - c. Placid water habitats — pools and holes.
    - d. Marginal areas.
  - 2. Interrupted habitats, with native biota.
    - e. Deposits—on rocks, etc.
    - f. Splash areas—on rocks
  - 3. Temporary habitats—transient and transitional, with varied biota.
    - g. Marginal pools.
    - h. Recession pools.

In the foregoing classification I have tried to recognize the important fact that the trout streams have a marked seasonal variation which emphatically affects the living organisms. In this respect the mountain streams do not differ from other aquatic bodies, which are also affected seasonally, and by the same factor, namely the spring floods.

A further criterion needs stressing. Both Steinmann and Thienemann make little distinction between what I have called native or endemic (or primary) organisms and invading (or secondary) organisms. Yet I believe this distinction requires emphasis. Certainly animals and plants found only in some small and isolated locality in one stream and not elsewhere can hardly be called endemic; similarly, insects the larval life of which is spent in quiet water and which in their adult stages visit the marginal pools, cannot be called native to mountain streams.

In Yellowstone River, for several miles below the outlet from Yellowstone Lake, there occur several species of plants, such as *Potamogeton, Myriophyllum,* and even some tiny patches of floating *Lemna.* This despite the fair current of the stream. But it is only in this locality that these plants occur at all. Farther down one never sees such plants. Yet below Yellowstone Falls there are considerable placid stretches where one might expect higher plants to effect a luxuriant growth; such, however, is not the case. No plants above the algae and mosses have been able to establish themselves.

Only those species can be said to be native or endemic which can exist under the average conditions offered by the particular ecological region. For ecological clarity, this distinction between what is primary and secondary, between what is native and what is foreign, between what is of constant and year round occurrence and what is temporary or transient, must be recognized. If not, then there is no purpose in ecological study of any sort, since then a sporadic or single occurrence would be of equivalent value to constant and wide-spread occurrence.

Quite logically it may be asked: Is there a criterion by means of which we can judge what life is endemic and what is foreign to mountain streams? Fortunately there is such a test which to a marked extent permits one to separate the native from the foreign biota. This criterion is the food, hence the stomach contents, of trout and other fish. Perhaps the food of stream insects should be considered also, since insects, aside from fish, constitute about 98% of the bulk of the stream fauna. At any rate, endemic species will be found *quite regularly* among the stomach contents and represented by *both their larval and adult stages,* or *at least the larval stages;* transients will be found only *intermittently* and *as adults.*

C. The Habitats. (Springs and Rills). As already noted, springs and their outlets received scant attention in this study. While physiographically continuous with mountain streams, they are physiologically separate. The following is summarized from Thienemann and Bornhauser. Bornhauser ('13) in a special study of springs groups them into two types—limnokren and rheokren. Rheokren are those springs from which the water flows away at the mouth,

Fig. 99. *Pteronarcys californica* nymphs on rocks, "emerging" from their nymphal skins. July 25, 1921.

Fig. 100. Rock and exuviae of *Acroneuria*. Oro Grande River, Idaho. July 3, 1924.

Fig. 101. Cluster of *Acroneuria* adults in crevice of rock. Yellowstone River. July 6, 1921.

Fig. 102. Stoneflies (*Acroneuria*) mating on shore grass along Yellowstone River. July 6, 1921.

down a hillside; there is no trace of any pool, just a direct outflow. Limnokren are springs which have a pool of varying size (Fig. 79). As characters for springs Bornhauser notes (a) constant renewal of "filtered," and hence "fresh" water, and (b) constant and low temperature. These two characters may be affected by altitude, age, the plants, temperature, environment (e.g., woods, open field), and food supply.

Thienemann ('12) classifies the fauna into three groupings for springs: (a) animals that are subterranean, (b) land forms and "moisture friends," (c) true spring forms. Bornhauser recognizes further distinctions among these types and groups them as follows: (a) Strange or foreign elements, (b) cosmopolites and ubiquists, (c) stream forms, (d) alpine forms (profound and boreal), (e) true spring forms, and (f) subterranean forms.

In the rills (Fig. 63) formed by spring outlets the fauna, according to Thienemann, agrees with that of the more quiet portions of mountain streams, i.e., that of the deposits and pools. From a physiographical standpoint such spring outlets are distinguishable by the stones which for the greater part are not submerged, but only moistened at their bases. Where such rills and outlets enter the stream proper, there one finds the repositories of trout eggs.

1. *Permanent Habitats.* These are the habitats which exist throughout the year, which neither the spring floods nor the summer droughts can extinguish. The same biota may be found here throughout the year. Mingled with it at times, chiefly at low water stage, one may find a foreign element, but such intrusion is rare. In these habitats the typical life of the mountain stream is found.

a. White Water.—Here are included the falls (Figs., 68, 74 and 88), cascades (Figs. 62, 66, and 89) and white rapids (Figs. 66, 68, 84 and 95) recognizable by the flow and color of the water. In falls the flow of the current is vertical, in cascades oblique, while in the white rapids it is a mixture of vertical, oblique, and horizontal flows. In falls and cascades the current flows chiefly in one direction; in white rapids the current is twisting, whirling, tumbling, hence simultaneously of many directions. Physiologically, one must note pressure and impact. Pressure arises from the volume of the water; impact refers to the force with which this volume strikes an opposed obstacle. As a result of the impact the water becomes white in color; this is merely the whiteness of the foam and of the air in solution. The water here is thoroughly saturated with oxygen, indeed, is really supersaturated. Impact and whitened waters, and hence a lack of transparency, are the more obvious characteristics of white water habitats.

Under such extreme and violent conditions one would hardly expect to find anything living at all. Yet curious to say, directly behind the falling water, and sometimes in the midst of it, if the volumes of water are not very large, one may find moss and bits of *Cladophora* caught in tiny crevices. In similar situations I have found Blepharoceridae larvae and pupae, and also the pupae of Deuterophlebia (Figs. 106 and 107). The distinct dorso-ventral flattening of the larvae and pupae, the powerful suckers which serve for attachment, and the very slow locomotion can be recognized as excellent adaptations.

Where large rocks extrude from the white rapids and are dashed with spray one also finds the adults of several species of Diptera running up and down the rock or sitting quietly in the spray (Fig. 114). These are the adults of Blepharoceridae, *Chamaedipsis* and *Philolutra* (Figs. 93, 108 and 114).

b. Clear rapids.—The clear rapids (Figs. 57 and 78) are distinguishable by the steadier flow of the water, the lack of opposed obstacles, and the transparency of the water. Typically they have a bottom of rounded, water-worn stones. An acoustic distinction might also be noted. Thus falls have a note of thunder, a deep bass; cascades have an overtone as of something rushing by: white rapids have a tearing, ripping sound; while the clear rapids have a laughing, bubbling tone.

This is the typical habitat of the mountain streams. Here the plants may find a hold on the immersed rocks. Here *Cladophora, Prasiola,* and *Nostoc* thrive. Here also *Oscillatoria* and *Melosira* may form films on the rocks, in which various rock diatoms grow abundant. Here, too, *Thremma* becomes prominent among Trichoptera, crawling about on the rock surfaces; while *Rhyacophila* and *Brachycentrus* fasten their cases in numbers on the upper surfaces of the rocks (Figs. 104 and 105). Behind and beneath the stones a luxuriant fauna and micro-flora appears. *Ulothrix, Melosira, Oscillatoria,* etc. form clumps in which smaller micro-organisms may establish a circumscribed residence. Blepharoceridae larvae (probably also *Deuterophlebia*) wander freely all over the stones. Groups of Trichoptera such as *Hydropsyche, Philopotamus, Goera,* etc. foregather between and under the rocks; flatworms such as *Polycelis* and *Dendrocoelium* lay their slime trails and feed on the micro-life; mayfly nymphs such as *Heptagenia, Ecdyurus, Iron, Ephemerella, Baetis* hunt diligently; and *Acroneuria* among stonefly nymphs finds this the optimal hunting-ground.

Here, too, trout of medium size like to establish their feeding ground, eating whatever the currents bring them, or picking suitable food off the rocks. Occasionally they will make quick forays into the white rapids. In precisely this sort of habitat I found bullheads in the Clearwater River in Idaho (opposite the mouth of the Wietas River); similarly in Glacier Park, in MacDonald Creek, just above its junction with the Flathead River, I observed *Cottus*. Suckers, too, may be found on rare occasion.

Where stones come sufficiently close to the surface, *Simulium* may settle and thrive. A thin film of water flowing over them seems their ideal requirement (see Thienemann, fauna hygropetrica). Where stones extend above the surface especially the larger stones, the adults of Blepharoceridae, etc., form the splash or "spray fauna" (Figs. 108 and 114).

All of these forms show some sort of adaptations. Either they are clingers in structure or by means of their housings, or they are strong swimmers. The clingers are quite generally flattened dorso-ventrally (*Polycelis, Dendrocoelium, Iron, Heptagenia, Acroneuria,* etc.), or their housings are attached (webs of *Philopotamus, Hydropsyche,* cases of *Brachycentrus, Rhyacophila,* etc.). The swimmers are more cylindrically built. Perhaps to call them "darters" would be more appropriate. For no animals truly swim in these rapids. Mostly, they hover behind some rock out of the way of the direct current, and dash or dart

forth quickly for the next promising shelter. This is the method of the young trout, also of older trout, of bullheads, of insects such as *Callibaetis* among mayflies, *Pteronarcys* among stoneflies.

c. Placid Water.—Where a depression occurs in the stream, the water tends to become placid (Figs. 58 and 82). The depression may be in the center or the side of the stream; it may be shallow, or very deep, but always distinctly beneath the average level of the stream. Usually the depressions are lined with rocks, quite generally larger in size than those in the clear rapids. These rocks become covered with deposits of various types of sediment after the spring floods, although the spring currents do not always wash them away entirely. Physiologically, there are the following conditions: quiet water, except for the surface current which is strong but smooth; because of this quiet there is less need for attachment; there is consequent liberty of locomotion. The temperature and the oxygen content are the same as in the clear rapids.

The plants of the pools, except for the tiny algae and diatoms noted in the clear rapids, are negligible. Despite the lack of deeper currents, there are no submerged or emergent plants. Among animals we find the larger fish seeking these pools which afford them freer movement. Of Crustacea there is *Cambarus* (found only in lower elevations, not in Yellowstone Park streams), *Pteronarcys californica* (Fig. 99) and the smaller stonefly nymphs. Occasionally one finds a rare ostracod and perhaps even a cladoceran or copepod. Among Protozoa the Vorticellidae find this an ideal environment, and may be found plentifully on the rocks. Thienemann lists various species of *Hydra* for such pools. I did not find any, probably because I failed to look for them. Caddisworms and mayfly nymphs are uncommon in the pools; but the smaller stoneflies and the large *Pteronarcys* seem to frequent the pools in preference to the more turbulent localities.

d. Marginal Areas.—Here the shores are referred to. The current is lateral in such places, with considerable friction by floating débris. Little bayous or inlets are sometimes formed, whose inhabitants are in part typically that of the clear rapids, in part that of other aquatic communities (springs, ponds). Surface skimmers prefer such areas. In streams of lower altitudes in Idaho I have found leeches, annulates (probably a *Limnodrilus*, sometimes a *Gammarus* or a *Hyalella*, and Hydroptilidae among Trichoptera in these shore or marginal areas. In addition, the moist soil affords abiding places for various surface breathing larvae, as of Tipulidae, Leptidae, Coleoptera, etc.

2. *Interrupted Habitats.* This division is admittedly arbitrary. It is characterized by being seasonal. While the habitats noted thus far may be found at all times of the year together with their biota, those falling under the present head are wiped out completely by the spring floods and must be repopulated or recolonized every year after the recession of the floods, when the currents are less violent. In fact, even during low water stages, during a summer freshet, a temporary flood of a few inches may wipe out the deposits. An interrupted existence is therefore characteristic of these habitats.

e. Deposits. The deposits on rocks (Figs. 71 and 83) and bottoms, and along the shores are formed by sediments after the spring floods. These sedi-

ments may be of varied composition, such as sand, mud, sulphur, etc. The spring floods remove these deposits completely, scouring the rocks until they are completely cleaned. As the floods recede, the deposits accumulate and the fauna is restocked in such places. Because of this annual interruption one can hardly speak of a resident fauna. Yet an abundance of smaller chironomid species establishes itself in these deposits together with most of the representatives of the micro-life noted under the clear rapids.

For European streams Thienemann notes the regular moss caps on the rocks, which during the spring floods are deeply covered with water, but emerge partly or completely during the summer droughts. In these moss caps may be found many Chironomidae, less motile types of mayfly nymphs, Trichoptera, Tipulidae larvae, *Atherix* larvae, the free living stages of parasites, Hydrachnida, etc., in fact a fauna that requires considerable protection and which can not exist in the mountain streams unless such protection (namely the moss caps) is present. In Yellowstone Park such moss caps occurred only in a few places along the Lamar (Fig. 72); in Idaho the Palouse River contains many such moss caps. In both places the fauna was much as described by Thienemann. Yet since these moss caps are rather the exception than the rule in the mountain streams of the Northwest, I am inclined to consider the biota as not truly native.

f. Splash Areas.—Like the deposits, these, too, are interrupted by the high water. They are the rocks that protrude from the water and are continually moistened by the spray. In this spray certain adults of Diptera (*Bibiocephala, Philolutra, Chamaedipsis*) run up and down, fly to the water's edge and then run up into the spray (Figs. 93, 108 and 114).

3. *Temporary Habitats.* These are habitats characterized by an invading fauna and flora. They can be regarded as both transitional and transient,—transitional as regards the type of organisms found, and transient as regards their existence. They are discontinued during high water or low water periods. The spring floods invariably wipe them out, and great recession of water will do the same (Figs. 54, 65, 71, 72, and 83). Perhaps no stream showed the relations of the regressive migration of the stream fauna together with the progressive invasion of foreign biota so typically as did the Lamar River. As the spring floods receded, sand was deposited copiously in the shore areas among the stones. In many places there were small pools and minor rapids, all connected by trickles (Figs. 75 and 76). The inhabitants migrated toward the deeper parts of the stream if possible; others, especially attached forms (*Rhyacophila, Brachycentrus*) became stranded or at least isolated; simultaneously, these pools became populated with various beetles, occasional Hemiptera (*Corixa, Notonecta*), copepods, Cladocera, and also various filamentous algae (*Spirogyra*, etc.), all of which are pond types. These pools were mosaic in their makeup; that is, only a few representatives of the pond communities were present in each pool; in fact, the pools differed strikingly among themselves. Later still, these recession areas dried up completely (Figs. 71 and 72) and various shore forms and scavengers appeared.

Fig. 103. Adult mayfly with a parasitic worm (*Mermis* sp.?) emerging from the caudal end. Enlarged eight times. Note the loop formed by the parasite within the abdomen of the insect. From confluence of Lava Creek and Gardiner River. Aug. 4, 1921.

Fig. 104. Stranded caddisworms (*Brachycentrus* and *Rhyacophila*). Lamar River. Aug. 8, 1921.

Fig. 105. Attachment of *Brachycentrus* cases. Some attached at caudal or small end others at broad or "mouth" end. Lamar River. July 25, 1921.

Fig. 106. Larva of *Bibiocephala*, enlarged 6 times. Note ventral suckers. From Snake River, Idaho. At right, pupae of *Bibiocephala*, showing variation in size and ventral attachments.

Fig. 107. *Bibiocephala* pupae. From Lamar River. Note the tubes of chironomids (*Tanytarsus?*) on the same rock. July 16, 1921.

Fig. 108. *Bibiocephala* adults as "splash flies." Oro Grande River, Idaho. Sept. 3, 1924.

Fig. 109. *Deuterophlebia* larva. Yellowstone River. July 30, 1921.

Fig. 110. *Simulium* sp. "Combs" of larva. x60.

g. Marginal Pools.—The foregoing described (h) the recession areas. The marginal pools can be primarily distinguished by their lateral connections with the stream proper. Generally there is some small trickle that leads into the pools (this includes the inlets or bayous of Thienemann), or there may be a broad lateral opening. At any rate, the current does not enter directly; hence there is a certain amount of quiet which permits less well adapted forms to establish themselves. These are primarily species of the lake shores, springs, and slow rivers. The fauna and flora can be called transitional, and is made up of elements from rapid streams as well as the other aquatic bodies noted. This is most notable in the types of Chironomidae, Trichoptera, and mayflies that establish themselves, but most typically by the surface skimmers that hunt in these spots.

The transition from stream to pond becomes marked in the various beaver ponds, especially where these engineers succeeded in damming some mountain creek. Such beaver ponds (Fig. 73) contain a rather sparse fauna, together with scattered pond plants. Among the animals, *Lestes*, *Enallagma*, and *Aeschna* among Odonata; various beetles; swimming Trichoptera (*Triaenodes*); *Notonecta* and *Corixa* among Hemiptera; and various semiaquatic Diptera are present in varying numbers. As a rule, the beavers keep the ponds too well cleaned to permit a rich pond life to establish itself. But at least some of the types are represented.

D. Adaptations to Mountain Stream Life. The difficulties of mountain stream life necessitate manifold adaptations on the part of the inhabitants. Steinmann in his earlier paper ('07) has outlined these so thoroughly that I can do no better than repeat them, with added instances. He lists seven types of adaptations:

1. Dorso-ventral flattening.—By appressed structure, as found in *Turbellaria*, leeches, *Ancylus*, stonefly nymphs, mayfly nymphs (*Iron*, *Heptagenia*, *Ecdyurus*). Many cases of Trichoptera (*Goera*, *Molanna*), Chironomus (*Tanytarsus*). Egg masses may be laid flat. The cocoons of leeches are flat. Pupae of Blepharoceridae and Deuterophlebiidae also are very flat.

2. Enlargement of adhesive surfaces, e. g., *Iron*, other Ephemeridae nymphs.

3. Small body compass, tendency to dwarfing. Noticeable only in plants.

4. Attachments: Temporary and permanent. Permanent: with cases, *Brachycentrus*, *Rhyacophila*, *Thremma*, *Glossosoma*, *Goera*, etc.; without cases, *Simulium*, leeches, snails, larvae of Blepharoceridae, etc. Temporary, by means of suckers, hooks, and anchors: various larvae of Diptera, Trichoptera, etc.

5. By weighting: web-spinning Trichoptera (*Hydropsyche*, etc.).

6. Reduction of swimming hairs, which are reduced in number or degenerate entirely.

7. Respiration. No surface breathers present.

Thienemann also notes an adaptation to temperature, namely the fact that the *Acarina* of mountain streams lay fewer, but larger eggs.

To this I would add a final adaptation in habit, namely that of the food eaten: the diet of inhabitants of mountain streams becomes generalized. Elsewhere (see

Muttkowski-Smith) this has been formulated as an axiom: the more specialized the conditions of the habitat, the more generalized the diet: the more generalized the conditions of the habitat, the more specialized the diet.

Dodds and Hisaw ('24 and '25) in their fine studies of the adaptations of insects to swift currents, reach conclusions similar to those of Steinmann and Thienemann.

FOOD RELATIONS

1. **Trout Food.** To arrive at a proper valuation of the stream population it was necessary to examine the stomach contents of the fish. In the following pages the stomach contents of a considerable number of trout are listed in tabular form. From the contents, an estimate of which is given in cubic centimeters, the bulk of the various food items may be inferred. To aid in this, the number of specimens of a species eaten is also listed.

TABLE NO. 1.—SHOWING FOOD OF TROUT (*Salmo clarkii*) FROM YELLOWSTONE RIVER. JUNE 28, 1921.

NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Contents in cc.	20	2	4	12	5	25	7	4	2.5	1	7	.5	2	4	5	10
Water Bait																
Limnephilus	20	..	3	..	5	20	3	3	1	..	2	..	..	4	4	..
Rhyacophila	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..
Hydropsyche	..	..	..	..	..	..	..	..	1	..	..	2	..	..	..	1
Pteronarcys	1	..	..	..	..	2	..	..	1	..	..	..	..	..	..	
Acroneuria	3	2	3	4	..	16	2	..	..	..	6	..	4	2	5	3
Baetis	1	..	..	..	..	..	2	..	..	1	..	..	..	..	..	..
Ephemerella	..	1	..	..	4	..	..	4	4	..	1	..	..	..	..	..
Drunella	..	..	..	..	..	2	..	..	..	..	4	..	1	..	..	..
Blepharocera 1	..	..	..	..	..	..	..	..	..	5	20	..	..	..	3	..
Nematodes	..	..	..	..	20	..	..	..	..	..	..	..	..	..	..	..
Tipulid lv.	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
Surface Bait																
Formica ad.	1	..	..	..	..	..	..	..	..	..	..	1	..	..	..	1
Lg. red ant	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Sm. black ant.	..	..	..	6	..	..	..	..	1	..	..	..	..	..	..	..
Vespa	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Bee	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
Simulium ad.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Culicid ad.	..	..	..	..	..	..	..	7	..	..	..	..	..	..	..	..
Plecia ad.	..	..	1	3	1	3	3	2	20	..	..	..	15	9	30	..
Mayfly	..	..	..	..	1	..	2	..	..	..	..	..	..	..	..	..
Cicada ad.	..	..	..	..	..	..	1	..	..	..	..	..	..	..	1	1
Lucanid ad.	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
Coccinellid ad.	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..
Cerambycid ad.	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..
Hydrophilid ad.	..	..	..	..	1	..	..	1	..	..	..	..	..	..	..	..
Scarabaeid ad.	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..

TABLE No. 2.—SHOWING THE FOOD OF TROUT (*Salmo clarkii*) FROM YELLOWSTONE RIVER

	June 29, 1921						June 30, 1921						
Number	1	2	3	4	5	6	1	2	3	4	5	6	7
Contents in cc	30	30	7	4	10	7	40	15	3	6	4	1	6
Pteronarcys lv	1	3	..	..	..	..	..	..	..	..	..	..	1
Acroneuria lv	28	23	8	4	16	6	4	8	1	6	4	2	1
Ephemerella nymph	..	..	4	..	..	..	..	..	5	1	..	..	3
Rhyacophila lv	..	..	1	..	1	3	..	..	1	..	..	..	..
Limnephilus	..	..	..	..	..	2	..	..	..	..	..	..	..
Formica ad	1	..	1	..	..	..	..	..	..	..	..	..	..
Plecia	..	..	1	8	2	20	..	..	..	..	..	..	..
Lympyrid ad	..	..	..	1	..	..	..	..	..	..	..	..	..
Hydropsyche lv	..	..	..	..	..	..	..	..	..	4	..	..	..
Black ant	..	..	..	..	..	..	..	..	1	1	..	..	..
Simulium ad	..	..	..	..	..	..	..	..	1	1	..	..	..
Culex ad	..	..	..	..	..	..	..	..	1	1	..	..	..
Plecia ad	..	..	..	..	..	..	..	..	44	4	..	..	..
Leptid ad	..	..	..	..	..	..	..	..	..	1	..	..	..
Muscid ad	..	..	..	..	..	..	..	..	..	1	..	..	..

TABLE No. 3.—SHOWING THE FOOD OF ONE TROUT TAKEN FROM YELLOWSTONE RIVER, JULY 6, 1921 BY MR. A. G. WHITNEY. CONTENTS ABOUT 25 CC.

Pteronarcys larva	1	Plecia	30
Acroneuria larva	4	Muscid ad	1
Acroneuria adult	10	Lucilia ad	1
Mayfly adult (Ameletus)	20	Enellagma female ad	1
Platyphylax ad	1	Raphidia ad	1
Simulium ad	1	Capsid ad	1
Winged ant	6	Cerambycid ad	1
Sawfly	1	Scarabaeid ad	1
Ichneumon	1	Lampyrid ad	1

TABLE No. 4.—SHOWING FOOD OF SMALL TROUT AND MINNOWS FROM THE LAMAR RIVER, JULY 7. 1921.

	Trout $1\frac{3}{4}$–$2\frac{3}{4}$ in. long												Minnows $1\frac{1}{4}$–$2\frac{1}{2}$ in. long				
Number	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5
Ameletus sp. small	1	...	1	4	...	1	1	1	1	1	1	1	...	...	...	...	...
Chironomus lv	...	...	...	...	1	1	1	1	1	1	1	1	...	...	...	...	...
Alloperla sp	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Ameletus sp	...	...	...	...	...	...	...	...	...	...	...	...	1	1	1	1	1
Chironomus sp	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1	..	1

Table No. 5.—Showing the Food of Cutthroat and Rainbow Trout from the Yellowstone River. July 13, 1921.

	1	2	3	4	5	6	7
Pteronarcys lv	....	5	....	1	....	....	.....
Pteronarcys ad	10	....	2	....	2	....	2
Acroneuria lv	....	....	....	....	....	4	.....
Acroneuria ad	2	....	2	....	....	2	3
Alloperla ad	1	....	....	....	....	....	.....
Bibiocephala ad	....	....	4	....	2	2	.....
Ameletus lv	....	....	....	....	....	3	1
Limnephilid ad	1	....	2	....	....	....	1
Black ant	1	....	....	....	1	1	.....
Green bee	1	....	....	....	....	....	.....
Cicada	....	3	....	....	....	....	.....
Cerambycid ad	....	....	....	....	....	1	.....
Wood chunks	....	4	....	....	....	....	.....
Young trout or sucker	....	....	....	....	....	....	1

The wood chunks were respectively 1 x 2 x 5 and 2 x 3 x 4 cm. The young fish eaten by number 7 was six inches in length.

Table No. 6.—Showing the Food of Native Trout from Yellowstone River at Mouth of Elk Creek. July 15, 1921.

	1	2	3	4	5	6	7	8
Pteronarcys adult	2	4	4	5	4	2	1	6
Acroneuria adult	....	3	4	4	2	2	4	.....
Bibiocephala adult	....	....	4	....	....	....	....	.....
Lestes ad. female	....	....	....	....	1	....	....	.....
Winged ant	1	....	1	....	....	....	....	.....

Number 3 had a copepod gill parasite.

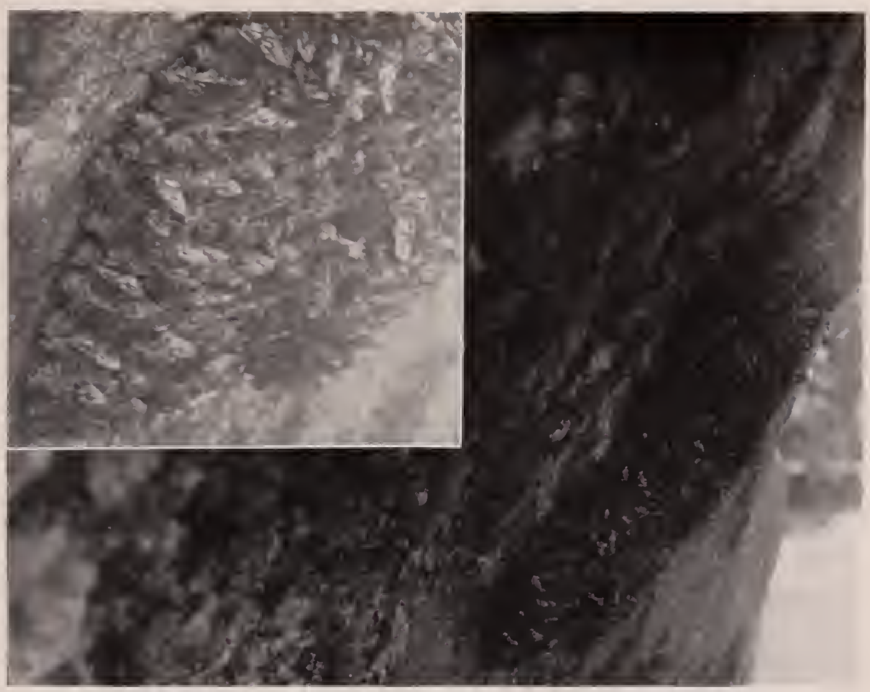

Fig. 111. *Atherix* cluster. Lamar River. July 22, 1921. The insert shows a section of the cluster enlarged x4.

Fig. 112. Rock where *Atherix* cluster had formed, on underside in cleft of rock. Lamar River, Aug. 7, 1921. On July 22, when the cluster was photographed, the sharp edge running from left to right was about twelve inches above the rapids.

Fig. 113. Tipulid larva, with inflated "baloon" at posterior end. Tower Creek. Aug. 29, 1921.

Fig. 114. "Spray flies" (*Chamaedipsis* and *Philolutra*) on rock in rapids. Lamar River. Aug. 31, 1921.

TABLE NO. 7.—SHOWING FOOD OF TROUT FROM YELLOWSTONE RIVER AT MOUTH OF ELK CREEK. JULY 16, 1921.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Pteronarcys ad...	2	5	1	5	4	3	5	4	1		1		3	2	2	2
Acroneuria ad....	2	5		4	1	5	3	1		3	5	1	2	1	2	1
Acroneuria lv....			2													
Hydropsyche lv..			1													
Hydropsyche pupa			1													
Hydropsyche ad..								6								
Ameletus ad.....			1	1								1				
Chironomus pupa.												1				
Plecia ad.........	1										4					
Tipula ad.........	1															
Tipula pupa......							1									
Pentatomid ad...							1									
Cicada ad.........							1									
Cerambycid ad...	1				1											
Scarabaeid ad....										1	1					
Black ant.........			4					8								
Red ant..........							5									
Argynnis ad......					1											
Attid spider......				1												

One of the specimens showed a Copepod parasite adhering to a gill.

Another contained a Nematode in its stomach. This may have been taken in with food or as a free-living stage of the parasite.

Besides the sixteen specimens noted above, twelve others were noted for their food content. In all cases the food comprised the two species of stone-flies. One specimen showed an adult *Lestes* sp.

TABLE NO. 8.—SHOWING THE FOOD OF TROUT FROM THE YELLOWSTONE RIVER, JULY 17, 1921. NUMBERS 1–11 FROM FOOT OF HOT SPRINGS NEAR THE "NEEDLES," NUMBERS 12–16 NEAR MOUTH OF ELK CREEK.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Pteronarcys ad...				1	2	1	1					2	3	1	1	2
Acroneuria ad....	1	2	3	4	4	3	4	5	1	2	3	4	7	3	5	6
Hydropsyche ad..		500														
Tipulid ad.......	1															
Chironomus pupa.	1															
Cicada ad........				1								1				
Ant..............										1		1				
Sawfly...........												1				
Enallagma ad....				1												
Carabid ad.......													1			

Number 2 contained a huge number of adult caddisflies, approximately 500 specimens.

TABLE NO. 9.—SHOWING FOOD OF NATIVE TROUT FROM YELLOWSTONE RIVER AT HELLROARING GAP. NUMBERS 1–10 COLLECTED BY MR. A. G. WHITNEY, THE OTHERS BY VARIOUS FISHERMEN.

	JULY 21, 1921										JULY 23, 1921				
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5
Pteronarcys ad.....	4	6	3	2	1	4	3	2	8	5	12	8	4	2	1
Acroneuria ad......	3	4	2	1	1	1	1	2	4	3	4	10	2	....	3
Noctuid moth......	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....
Hydropsyche ad....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....

July 24, 1921. Lamar River. Trout collected by Mr. Henry Lambert. Three specimens, each with one minnow in stomach. No other contents.

July 25, 1921. Yellowstone River. Trout collected by fisherman. Two specimens noted, each containing a minnow.

August 1, 1921. Yellowstone River, at Cooke City bridge. Three trout noted feeding on caddises of *Rhyacophila.*

August 1, 1921. Lamar River. One native trout with two *Doroneuria* and two grasshoppers.

August 8, 1921. Lamar River. Two trout, each with two grasshoppers.

August 11, 1921. Yellowstone River. Trout taken by Mr. Arnold Whitehouse at hot springs near the "Needles."

	1	2	3	4	5	6	7	8	9	10	11	12
Ameletus lv..........................	3	3	....	3	2	2	....	....	....	....	....	1
Caddises..............................	....	....	2	....	....	....	....	....	....	....	....	....
Acroneuria lv.........................	....	....	....	....	....	....	....	....	1	1	....	....
Grasshopper..........................	....	....	....	1	2	2	1	1	....	....	1	....

August 11, 1921. Slough Creek. Two specimens gathered by Mr. Robert Hallenberg, one containing a field mouse, the other a green frog.

August 13, 1921. Yellowstone River. Two specimens collected by fishermen, one containing 3 *Ameletus* and 10 *Simulium* larvae, the second with about 200 *Simulium* larvae.

These 148 stomachs represent only a portion of those examined, probably about one third. Since the others were practically identical as to their contents it was not considered worth while to list them all individually. Toward the middle of the summer only such specimens were noted as had fed on unusual food, such as mice, frogs, pieces of wood, or on one type of food primarily.

From the listed data it will be seen that it is possible to follow the summer history of the fish food, beginning with the spring floods, the summer lapse,

and the autumnal re-stocking of the streams. The general history has been outlined in an earlier paper: "The Food of Trout in Yellowstone National Park" (Muttkowski, '25). Certain conclusions offered in that paper are relavant and are quoted here: "From the examination of fish stomachs it is possible to deduce much about the food habits of fish. First, fish will take food that is easily captured; secondly, that which is accessible with difficulty; and lastly, strange and unusual food. Of the food available in mountain streams, stoneflies and mayflies are most easily obtained and constitute the major portion of the food eaten. Here, too, the eggs, fry and fingerlings should be listed, as fish are cannibals when opportunity offers; and trout are no exception, but will eat other fish just as greedily as will bass. Caddisflies, well protected by virtue of their tough attached cases, and moreover, even more inaccessible on account of the appressed structure of many cases, rank in the second category, and for that reason constitute a much smaller item of fish food than the other two groups of insects. However, they are used extensively as food by the stoneflies and mayflies, and in this respect become as important, though indirectly so, as their enemies. Among strange and unusual foods can be listed the surface bait.

"In general, fish are opportunists as far as their food is concerned. They eat what animal food is available, regardless of the origin. As a result, if one knows the animal life of a particular region, one can tell from the stomach contents where a fish has fed. In a lake, for instance, the plant and animal life is distributed in regular 'zones,' most animals limiting themselves to particular depths. Some are found only on the shores, others on the vegetation in the shallows, still others, only in the muck at considerable depths. With a knowledge of the animals found in these various zones it is possible to learn a good deal about the food habits of a fish, his migrations, and his preferences.

"On the whole, fish are indiscriminate in their choice of food as far as quality is concerned. They like to feed in a particular region, and stay there until satiated. Thus, when feeding from plants, they eat whatever they can find there; and once they begin to feed from plants they continue feeding there until their hunger is satisfied. At periods of plentiful food, fish do not migrate while feeding.

"Curious to say, it often happens that a fish may find a certain type of food so much to his liking that he will seek only that type. This may be worms, leeches, snails, back swimmers, caddis-worms, or other kinds. Thus, we may find stomachs filled with dozens of individuals of one type of animal, such as crayfish or snails. Even more striking, one may find stomachs filled with highly distinctive cases of some particular species of caddis-worm.

"This predilection for some particular food is more often observed in the case of surface food than in water bait. I have found fish stomachs, including trout stomachs, gorged with hundreds of specimens of a single type, such as ants, grasshoppers, dragon flies, caddisflies, orl flies, mayflies, midges, etc., indicating that the particular fish had taken a fancy to this special type of food, and had hunted assiduously for the delicacy. There is nothing abnormal in such a predilection, not more so than in the case of a boy who makes a meal

off desserts, be it ice cream, or fruit, or cake. But right there, in the longing for the unusual, lies the weakness of the feeding habits of fish, the trait which lays them open to capture by the angler. Since the unusual attracts, anglers have made use of this phenomenon in the types of flies selected by them.

"A fish is easily deceived, for he is not very observant. His eyesight is poor and he recognizes things chiefly through their movements. For instance when an angler uses a fly, the fish is supposedly deceived by three factors,—form, pattern, and movement. In the matter of form and pattern the fish's vision is too weak and nearsighted to recognize the bait for what it is. He is used to certain distorted images which impress him more through motion than by any other factor, and he captures or tries to capture such a moving object. But it is also the unfamiliar, the unusual, which tempts fish, perhaps more than the customary objects. How else can one explain the presence of blocks of wood, of straws, twigs, leaves and the like, in fishes' stomachs? On more than a dozen occasions I have found blocks of wood in trout stomachs. In at least half the cases there was not the remotest resemblance in the shape of the block to any type of surface bait. An irregular cube has no resemblance to any insect, while an oblong bit might well have the approximate outline of a stonefly or a grasshopper. But it was probably the strangeness, the unusualness of the block of wood which attracted and tempted the trout. The most interesting feature of these instances was that in only one case were the blocks of wood taken by a hungry fish; that is, only once were the blocks of wood the sole stomach content. In all other instances, blocks and sticks were gulped by fairly well-fed fish. One might say that they were taken as a sort of salad or dessert, indicating that their novelty tempted the fish."

2. **Insect Food.** A special study of the food of the insects was made possible by the collaboration of Dr. Gilbert M. Smith, then of the University of Wisconsin, who arrived early in August. Specimens were obtained from each of the four type streams and their stomach contents studied, Dr. Smith identifying the plant organisms and the writer the animal life. The results of this particular collaboration are published in a separate paper (Muttkowski-Smith: The Food of Trout Stream Insects in Yellowstone National Park, Roosevelt Wild Life Annals, Vol. 2, No. 2).

For the purpose of the present paper the following may be noted from the summaries given in the collaboration:

TABLE NO. 10. SHOWING THE SUMMARIES OF FOOD OF TROUT STREAM INSECTS. YELLOWSTONE PARK, 1921.

NAME	Number of specimens		Animal food %	Plant food %	Detritus %
Perloidea					
—Pteronarcys	26		3.85	53.85	42.3
—Acroneuria	49		77.4	6.3	16.3
—Perla	5		85.	15.	....
Average for	80	=	54.	22.3	23.7
Ephemeroidea					
—Ameletus	25		....	22.7	77.3
—Baetis sp	2		....	50.	50.
—Drunella	20		18.5	36.8	44.7
—Ephemerella	28		3.7	36.3	60
—Heptagenia	34		....	24.	76.
Average for	109	=	4.3	29.7	66.
Trichoptera					
—Rhyacophila	32		49	23.	28.
—Hydropsyche	27		42.	54.3	3.7
—Brachycentrus	33		18.3	72.7	9.
—Thremma	23		....	64.	36.
Average for	105	=	28	54.	18.
Diptera					
—Chironomidae	6		....	71.	29.
—Simulium	14		....	79.	21.
Average for	20	=		76.6	23.4

"Even from so brief a study as the foregoing certain facts can be gleaned. The most notable point is that aquatic insects in rapid streams are opportunists as regards food, and eat whatever is available. Secondary to this is the fact that the aquatic insects forage extensively, i.e., migrate freely in search of food.

"Both of these points become evident from the collections made in Lost Creek, where special efforts were made to select various spots in the creek for sample collections of food and of specimens in the vicinity or upon that food. Reference to the stomach contents of the individual specimens and comparison with the food items listed for the particular spot shows at once that the large majority of specimens contained food that did not occur within many feet of the particular locality. This indicates that these species must be rovers and foragers to a marked extent, and that they are opportunists on the whole and eat whatever is available.

"Environmental conditions in mountain streams are strenuous; the strong current in particular makes life somewhat precarious and selective feeding difficult. Hence as a result the diet becomes diversified; the insects take whatever comes along, be it plant, detritus, or animal matter. Their diet thus becomes

Fig. 115. Parnidae larva. *Psephenus lecontei* enlarged x10. From Lake Mendota, Wis.

Fig. 116. Parnidae larva. *Elmis vittatus* enlarged x10. From Lake Mendota, Wis.

much more generalized than the diet of related species in more permissive habitats, such as ponds and slow streams. In the latter the less strenuous conditions permit the insects to select their food, that is, to restrict their diet to favored food, and to search for that food.

"In other words, specialization of habitat leads to diversification of diet (i. e., generalization of diet), while generalization of habitat permits a restriction of diet, (i. e., specialization of diet)."

3. **The Seasonal Food Cycle.** Here, too, I prefer to quote from a prior paper (The Food of Trout in Yellowstone Park): "Besides these main items of the normal trout diet in the mountain streams, the so-called 'water bait,' there is the surface drift or surface bait of water-trapped animals, chiefly insects. This comprises especially the weak fliers such as moths, ants and grasshoppers, while spiders, centipeds, mice and other animals may occur. But the life of a trout stream is dependent on its normal inhabitants, not on the odds and ends which a kind wind or accident may provide. It is only during the brief summer period that surface bait becomes important; and for a period of four to six weeks the fish are largely dependent on this type of food for their existence. That the emergence of their natural water bait, with the resulting depletion of this primary food supply, should be synchronous with the summer flights of ants, moths, grasshoppers and other poor fliers that are easily water-trapped, is one of many instances of the admirable provisions of nature.

"Indeed, this is carried still further at this period. At this time the minute life of the shore waters, especially the shore diatoms, flat-worms, chironomids, and the young stages of mayflies, stoneflies and caddisflies, receives a tremendous impulse and becomes quite prominent. At this period also the young of trout, suckers and other fish in the mountain streams can be found in the shore pools and shallow rapids feeding on the minute organisms in these places. Here lies the remarkable coincidence: the simultaneous appearance and growth of fish fry and of a protected food supply for its use. For the older trout are unable to get into these shallows, which therefore offer both protection and food to the young fish.

"From the foregoing it is evident that there exist only two well-marked periods in the annual cycle of mountain trout streams, namely, a 'water food' period covering nearly eleven months of the year, and a 'surface food' period occurring during the summer, and lasting from four to six weeks. This is the period when trout, as anglers put it, 'rise to bait.' These same periods might also be called flood and ebb periods, or flood and drought periods, from the fact that high water lasts from October to July, while the ebb or low water stage of the summer is really very brief.

"With the fall rains the brief low water stage ceases and the conditions revert to those existing during winter and spring, and continue to the time of emergence described, that is, about the first week of July."

COMPARISONS AND SUMMARIES

Definition of Mountain Stream. Steinmann ('12, p. 125) in his fine paper on alpine streams offered the following summary:

1. Conditions and character of mountain streams are:
   a. Constant and low temperature.
   b. Strong current and marked changes in volume of water.
   c. Rich oxygen content.
   d. Paucity of plants.
   e. Stony bottoms.
2. These characters impress the animal world as follows:
   a. Composed of resistant cosmopolites and stenothermic freshwater forms.
   b. Body shape; morphological adaptations, arrangements for attachment holdfasts, dorsoventral flattening, dwarfing, etc.
   c. Life: low food requirements, embryonic development prolonged.
3. The fauna consists of
   a. Cosmopolites, ubiquists.
   b. Torrenticolar-profound elements.
   c. True stream animals.
4. The fauna is composed of forms which originally belonged to still water. The influence of stream life is recognizable to a different extent in each form.
5. All true mountain stream forms can be regarded as glacial relicts, since they agree more or less closely with Zschokke's postulates in their:
   a. Simultaneous occurrence in mountains in the north.
   b. Simultaneous occurrence in mountains and in lake depths.
   c. Absence from the warm, still and slow moving waters of plains.
   d. Reproduction during low temperature.

This characterization, while very excellent so far as the fauna is concerned, is primarily intrinsic, in that it stresses the responses of the animals rather than the extrinsic factors which elicit this response. In the present study I have attempted to outline what these external factors are. Based on the data presented, the following definition of the mountain stream as an ecological unit, including both positive and negative characters, is offered:

I. Physiographical Characters.

Positive.	Negative.
1. Constant and considerable change in elevation.	
2. Slight depth.	
3. Great and successive changes in types of bottoms.	
4. Volume of water relatively small, but impact very great.	

II. Physiological Characters.

Positive.	Negative.
1. Strong and rapid current, resulting in	1. Uninfluenced by winds.
2. Equal distribution (=circulation) of;	2. Do not freeze over in winter.
a. Low and constant temperature.	
b. High oxygen content.	3. No stratification of temperature and oxygen content. Hence no thermocline.
c. Substances in solution, affecting the chemical composition.	
d. Substances in suspension, affecting the turbidity or transparency.	

III. Ecological Characters.

1. Types of habitats.	
a. Permanent, with native biota: white water, clear rapids, placid water, marginal areas.	
b. Interrupted, with native biota: deposits, splash areas.	
c. Temporary, with transient and transitional biota: marginal pools, recession areas.	
2. Distribution of habitats linear or horizontal, all types intermixed.	—No vertical distribution of habitats into zones, as in lakes and slow streams.
3. Plant life confined to algae and mosses; clinging types.	—No emergent vegetation, no higher plants.
4. Animal life.	
a. Respiration: all water breathers.	—Surface-breathers absent.
b. Locomotion: chiefly clingers and crawlers. Swimmers move in "leaps."	—Free swimmers few. Burrowers are scarce.
c. Structural: usually well protected by armor, cases, and webs.	—Soft-bodied forms rare.
d. Composition: stoneflies, Blepharoceridae, Tricladida, are most characteristic Invertebrates, trout most characteristic Vertebrates.	—Plankton organisms absent, Crustacea and Annulata rare. No Amphibia.
e. Food habits generalized, other habits specialized.	

Even a superficial examination of these characteristics shows clearly that whatever variability exists in different parts of a mountain stream is due to physiographical factors; the physiological factors are quite constant. In this respect the mountain stream as an ecological unit is outstandingly different from other units, since in these the physiological factors are variable, and the physiographical ones quite constant.

Of physiological factors only the current varies, a condition which depends entirely on the physiography. All other factors are relatively constant; thus temperature, oxygen content, speed of circulation, chemical makeup, all tend to be alike in all parts of a specific mountain stream.

Another characteristic is that these conditions are distributed horizontally, namely, there is no vertical distribution, and hence a lack of the zonation one finds in other ecological units.

Other Aquatic Bodies. As already noted, in this study the factors of the environment have been stressed rather than the responses of the organisms to these factors, since it is only through the study of these factors that the responses can be understood. The following table is an attempt to present in comparative form the factors that affect the various aquatic habitats, and the chief responses to these factors. The arrangement is based on personal studies covering some twenty years.

TABLE NO. 11. Showing in comparative form the factors which affect the various aquatic habitats and the chief responses to these factors.

	Mountain stream	Lake shores	Lake depths	Springs	Slow streams	Shallow lakes and ponds	Swamps	Bogs
I. PHYSIOGRAPHY								
Descent in altitude	*considerable*	very little	none	slight	*very gradual*	none	none	none
Bottoms	*constantly changing*	more regular	*regular, in zones*	fair variety	fair variety	fair variety	less variety	least variety
Depth	*never great*	little to great	*often very great*	shallow	often deep	little	little	*very shallow*
II. PHYSIOLOGY								
1. Extrinsic								
Volume and impact	*very violent*	*violent*	variable	very slight	slight	slight	slight	none
Wind and pressure	no influence	*great influence, causes waves*	little, very gradual in its effect	slight	slight	slight	slight	none
Current	*continuous, strong* seasonal variation	*intermittent daily variation*	chiefly convection, *intermittent, fall "overturn."*	*constant through year*	constant, slight	convection	convection	none
Chemical								
in sol.-chem. comp.	*equal distribution*	*unequal, varies daily*	*unequal, varies slowly*	equal distr	unequal	unequal	unequal	unequal
in suspension = turbidity and transparency	*equal throughout stream*	*unequal, varies daily*	*unequal, varies seasonally*	equal throughout	unequal	unequal	unequal	unequal
Light	same throughout	same throughout	*less light with increase in depth*	same throughout	variable	variable	variable	same throughout
Temperature	*constant, low throughout year, never freezes over*	*very changeable, varies daily, freezes over*	varies slowly, seasonally freezes at surface	*constant and low through year, do not freeze*	*varies seasonally* freeze over	*varies in seasons* freeze over	*varies daily* freeze	*varies daily* freeze
Oxygen	*high aeration throughout year*	*daily variation high content*	*slow variation, decrease in summer*	*high content*	*varies slowly*	varies daily	varies	varies
Circulation	*complete, by falling*	*complete by winds*	*incomplete; stratification to form Thermocline*	*complete, by churning*	incomplete, convection and winds	complete, winds	incomplete, convection and winds	incomplete, convection only
2. Intrinsic								
Respiration	*water-breathers only*	*water-breathers only*	*water-breathers only*	water and surface breathers	both types	both types	*more surface breathers*	*chiefly surface breathers*
Locomotion								
Swimmers	few fish and insects	few fish and insects	many fish, insects	few insects	fish and insects	fish and insects	insects	rare swimmers
Clingers and crawlers	most animals	most animals	fewer	chiefly these	few, on bottoms	few, on plants	many, on plants	rare
Burrowers	very rare	very few	very abundant	few	very common	common	common	common
Food habits	*generalized*	*generalized*	specialized food	*generalized*	specialized	specialized	specialized	specialized
Structural	*appressed*	*appressed*	cylindrical	varied	varied	varied	varied	varied
3. Habitats								
Arrangements	*intermixed*	more regular	*regular, in zone*	fairly orderly	orderly	orderly	*intermixed*	*no order*
Distribution	*horizontal*	*horizontal and vertical*	*vertical*	hor. and vert	hor. and vert	hor. and vert.	*horizontal*	*horizontal*

TABLE No. 11. (*Continued*)

	Mountain stream	Lake shores	Lake depths	Springs	Slow streams	Shallow lakes and ponds	Swamps	Bogs
III. PLANTS								
Emergent	*none*	*none*	*none*	few	few	many	chiefly	chiefly
Floating	*none*	*none*	*none*	few	few	common	*very common*	common
Submerged	*few*	*few*	many	*few*	many	many	*common*	few
Algae	frequent	few	*many*	few	many	*common*	*common*	common
Mosses	rare	none	none	few	few	few	few	*common*
Higher plants	none	none	*common*	some	many	*abundant*	*abundant*	abundant
IV. ANIMALS								
Protozoa	few	few	*common*	few	*common*	*abundant*	*abundant*	abundant
Hydrozoa	rare	none	*abundant*	few	*common*	*common*	few	few
Platyhelmia	common	common	common	common	fewer	fewer	fewer	fewer
Nemathelminthes	rare	rare	common	few	common	common	common	common
Rotifera	rare	rare	common	few	common	common	common	few
Annulata	rare	few	common	few	common	common	common	few
Leeches	rare	*common*	few	few	frequent	*common*	frequent	few
Mollusca	rare	frequent	common	common	common	common	common	few
Bryozoa	none	none	common	rare	common	common	few	none
Decapoda	rare	rare	common	common	common	common	common	rare
Plankton	none	little	common	rare	common	common	common	frequent
Other crustacea	rare	few	common	common	common	common	few	rare
Araneae	none	none	none	rare	few	*common*	*common*	few
Hydrachnida	rare	rare	common	rare	common	common	common	rare
Ephemeroidea	common	common	common	rare	common	common	common	rare
Odonata	rare	rare	none	rare	common	common	common	rare
Hemiptera	none	few	few	common	common	common	common	few
Neuroptera	none	none	few	none	few	*common*	*common*	none
Lepidoptera	none	none	none	rare	few	*common*	*common*	none
Trichoptera	common	common	common	common	common	common	common	rare
Simuliidae	*common*	none	none	some	none	none	none	none
Blepharoceridae and Deuterophlebiidae	*common*	none	none	few	none	none	none	none
Chironomidae	common	common	common	common	common	common	common	common
Corethridae	none	none	*common*	none	none	*common*	none	none
Psychodidae	rare	rare	none	rare	rare	*common*	*common*	*common*
Leptidae	frequent	none	none	frequent	*common*	*common*	rare	none
Tipulidae	rare	rare	none	frequent	common	common	common	frequent
Dytiscidae	none	none	rare	none	common	common	common	none
Gyrinidae	none	rare	none	rare	*common*	*common*	frequent	none
Dryopidae	rare	*common*	none	frequent	none	none	none	none
Perloidea	*common*	rare	none	rare	none	none	none	none
Salmonidae	*common*	frequent	frequent	none	none	none	none	none
Cyprinidae	none	few	common	rare	common	common	few	none
Amphibia	none	rare	none	few	common	common	common	few

From the table it would be possible to list separately the characteristics of each type of aquatic habitat. But since these are already emphasized in the table by italics, it would be mere repetition to go through such a procedure.

In so far as the main work of this study is concerned, it is frankly admitted that the results are by no means complete, or even remotely so. The streams of the Northwest, in fact, throughout the United States, offer a multitude of problems which need prolonged investigation. If the present paper succeeds even to a slight extent in stimulating interest and study of some of these problems, it will be a recompense for the considerable effort, time, and money spent by the writer and other agencies noted in the introduction, in carrying on the present study.

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THE FOOD OF TROUT STREAM INSECTS IN YELLOWSTONE NATIONAL PARK

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CONTENTS

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INTRODUCTION

The present collaboration is based on certain joint investigations of the authors in Yellowstone National Park during the summer of 1921, under the direction of the Roosevelt Wild Life Forest Experiment Station, of the New York State College of Forestry at Syracuse. During that summer the senior author was engaged in the study of the broader problem of the ecology of trout stream organisms. In considering the trout stream as an ecological unit, it was necessary to study the biota not merely as related to trout, hence as a potential food supply, but also as related to each other. In other words, what is the food supply of the various animals inhabiting the trout streams?

For the study of this phase it was necessary to make a survey of the plant life of the streams and the part it plays in the food of the animals. For obviously, in the last analysis, all life in trout streams, quite as much as elsewhere, is dependent on the plant life. This phase was taken up more intensively after the arrival of the junior author in Yellowstone Park in early August, when collections were made of the plants of different streams together with associated animals. Collections were made from different parts of the streams in order to obtain as varied a series of selections as possible in these highly specialized habitats. For instance, from Lost Creek samples of plant life were obtained from the swiftest rapids, from the pools formed by the rapids, from relatively quiet waters, from exposed and shaded spots, and also from the lateral pools.

Specimens were collected jointly from four streams typifying the various kinds of trout streams found in Yellowstone Park,—indeed, found throughout the Northwest. These are: 1. Yellowstone River, typical of the larger and permanent rapid streams; 2. Lamar River, a good type of "variable" or fluctuating stream, carrying enormous masses of water for short periods, followed by equally short periods of rapid recession—on the whole, a stream with a relatively low, equable flow; 3. Lost Creek and Tower Creek, both precipitous mountain streams of rather short length, with many falls and rapids. Their type is very numerous and form the tributaries of the larger streams. Tower Creek is the best representative of this type; but Lost Creek, a smaller stream, comprises similar conditions and biota, and was selected because of its convenient location at Camp Roosevelt, our field base.

In each case two comprehensive survey collections were made covering as many different habitats as the stream seemed to offer. Besides these, a number of isolated collections made previously by the senior author were available for comparison. The collected material was studied while still fresh. This applied also to the stomach contents of the various insects.

In the following pages, the notes on animals are by the senior author, those on plants mainly by the junior author.

DESCRIPTION OF LOCALITIES

Yellowstone River, within Yellowstone National Park, has a continuous fall, thereby increasing the force of its current enormously. Generally the current attains a speed of eight to ten miles per hour, in places up to twenty miles. The many rapids, short and long falls and the tortuous bed, make the stream unnavigable within the Park. In width it varies from fifty to three hundred feet, especially in the "eddies" where the waters are dammed somewhat by the inflow of some tributary. The depth may be considerable, some of the "holes" attaining thirty and even forty feet, and rarely less than six feet, except for a few fords. The bed of the stream contains many huge boulders, granite rocks, and smaller stones. Hardly anywhere along the Yellowstone does one find sand or gravel except in the interstices between the huge boulders and lesser stones along parts of shores that are less directly exposed to the current.

The shores of the Yellowstone are greatly varied, from volcanic rock to alluvial and glacial soil, the latter with the "sulphur slides" so characteristic of the canyons of the Yellowstone. In the spring the melting snow carries great quantities of this soil into the stream which then silts out as the period of high water passes. Such slides may, however, occur at any time in the summer and the river will then be turbid for a few hours or days, until the loose soil has settled or is washed away.

The Lamar River varies from fifty to one hundred and fifty feet in width, and at the ordinary stage is about two feet in depth. Its rapids are of a much milder type than those of the Yellowstone, although during the flood period they rage with tremendous force and appear formidable. In spring the melting snows bring enormous masses of mud and sand with them, which silt out among the shore rocks and boulders as the waters recede,—in fact, nearly covering the rocks and thus giving little idea of the ferocity of the spring torrents. Yet each year, with the spring floods, all these deposits are washed out, to be replaced by others coming down from the mountains.

The bed of the stream is generally clear, composed of granite boulders, and rocks usually not smaller than a cubic foot, but of smaller size at the fords. The Lamar is essentially a shallow stream and fordable in numerous places. Yet it is an excellent stream for trout and supports a rather luxuriant plant and animal life.

The precipitous streams, such as Lost Creek and Tower Creek, because of their great vertical fall, have few cobble stones or gravel or sand in their beds, except at the margin of the pools. Tower Creek is of practically constant width, about twenty to twenty-five feet, for at least seven miles above the falls, the junction point with the Yellowstone. The depth varies from eighteen inches to two feet. The bed is nearly uniformly composed of rounded cobbles varying from pebble size to a cubic foot, with some huge boulders scattered along the bed and shores of the stream.

Lost Creek is ideal for the study of the recession of waters. In flood periods (late June) it is an energetic and precipitous torrent which impresses one by the

amount and force of the descending waters. A few weeks later, in middle August, the creek is a thin trickle carrying a flow of hardly more than a gallon per second. Even this disappears entirely into the ground about five hundred yards below the pretty Lost Creek Falls in a bed of mixed gravel and cobbles, a short distance above Tower Fall Junction Ranger Station. Half a mile down the stream reappears as a sump along the Cooke City road, leading down to the Cooke City bridge across the Yellowstone River.

THE PLANTS AND ANIMALS

General Factors. In such a highly specialized habitat as mountain trout streams both physiographical and physiological conditions act restrictively on the biota. The constant fall of the water and the resulting tremendous force of the current constitute the major factors in limiting the aquatic population. Secure places for temporary attachment are few: shelters against the current are none too many; there is little opportunity for swimming. Hence only plants and animals with holdfasts,—either natural or artificial, such as webs, claws, suckers —or powerful swimmers can establish and maintain themselves. In addition, the force of the water makes their resting places rather uncertain, since offal, sticks, and stones are constantly being whirled along and strike against the rocks. Even larger rocks may be moved by the current; indeed, well into the summer, weeks after the spring floods are over, one can hear the slow rubbing and grinding of the rocks in the stream beds.

On the other hand, the speed of the water, and the frequent rapids and falls make for high oxygen content. Most of the fauna seem to require this. If for any reason the oxygen is diminished, or the constant flow ceases, the animals die.

Due to these influences, the fauna is surprisingly sparse in all of the streams—that is, in number of species, but not in number of individuals of each species. The specialized conditions limit the number of species; but they also tend to increase the numbers of individuals of a species vastly. Hence one finds the endemic forms present in astonishing numbers.

The major portion of the fauna is composed of insects, to exceed 99%,—that is, if fish be excluded. One is surprised at the almost complete absence of Annelids, leeches, Crustacea, and Mollusca, and at the rarity of Protozoa and Rotifera, all of which are so abundant under less violent aquatic conditions.

The plants are restricted to algae; all higher plants are absent. Smaller algae, diatoms and desmids find shelter in tiny crevices, in the films of emergent shore rocks, or behind rocks where the current is not too strong.

Certain faunistic peculiarities of the streams may be noted. Thus, both Tower Creek and Lost Creek are characterized by the abundance of planarians and of the caddisworm *Hydropsyche*, and by the nearly total absence of *Simulium*. On the other hand, *Simulium* is present in quantities in the Yellowstone and the Lamar rivers, while planarians are exceedingly rare. The larger *Perloidea* are also very characteristic for these two streams. In smaller and precipitous streams they seem to be somewhat infrequent.

List of Biota.

Algae and Diatoms.

Cladophora sp.
Closterium sp.
Cocconeis sp.
Epithemia sp.
Gomphonema sp.
Melosira sp.
Nostoc sp.
Oscillatoria sp
Prasiola sp.
Rhoicosphenium sp.
Rhizoclonium sp.
Spirogyra sp.
Synedra sp.
(Moss—undetermined)

Animals.

Protozoa
- *Ameba* sp.
- *Colpoda* sp.
- *Gregarina* sp.—as parasites in Trichoptera, Perloidea, and Ephemeroidea.

Rotifera
- Several spp.

Nematoda
- *Mermis* (?) sp.—as parasites in mayfly nymphs and in *Simulium*.

Arthropoda

Perloidea.
- *Pteronarcys californica*
- *Pteronarcella badia*
- *Acroneuria pacifica*
- *Alloperla coloradensis*
- *Alloperla fidelis*
- *Alloperla lineosa*
- *Alloperla* sp.
- *Doroneuria theodora*
- *Isoperla 5-punctata*
- *Perla verticalis*
- *Perlodes signata*
- *Pteronarcella badia*
- *Pteronarcys californica*

Ephemeroidea
- *Ameletus* sp.
- *Baetis* sp.
- *Callibaetis* sp.
- *Drunella grandis*
- *Ephemerella coloradensis*
- *Ephemerella* sp.
- *Heptagenia* sp.
- *Iron longimanus*

Trichoptera
- *Brachycentrus* sp.
- *Glossosoma* sp.
- *Goera* sp.
- *Hydropsyche* sp.
- *Limnophilus* sp.
- *Neophylax concinnus*
- *Philopotamus* sp.
- *Platyphylax* sp.
- *Rhyacophila torva*
- *Thremma* sp.
- *Triaenodes* sp.

Diptera
- *Atherix variegata*
- *Bibiocephala comstocki*
- *Bibiocephala grandis*
- *Chamaedipsis* sp.
- *Chironomus* sp.
- *Cricotopus varipes*
- *Metriocnemus* sp.
- *Orthocladius* sp.
- *Philolutra simplex*
- *Procladius* sp.
- *Psychoda* sp.
- *Rhamphomyia* sp.
- *Simulium* sp.
- *Tanytarsus exiguus*

THE FOOD OF THE INSECTS IN TROUT STREAMS

In the following tables the first numbers are the collection numbers. The succeeding number refers to the individual insect whose stomach contents are listed. The estimates are given in percentages. "Detritus" signifies unidentifiable refuse. The figures in parenthesis are the numbers of individual items of food.

The Food of Perloidea or Stoneflies. The table below gives in detail the food percentage of the stoneflies as determined from the specimens examined.

TABLE NO. 1.—SHOWING THE FOOD OF THE PERLOIDEA OR STONEFLIES.

Collection Number	Number and Name of Individual Specimens	Date 1921	Locality	Habitat	Food Items in Percentages
5517	1. Pteronarcys californica..	July 5	Yellowstone R.	Rapids near shore.	Intestines with wood fibers, 100.
5517	2. Pteronarcys californica..	July 5	Yellowstone R.	Rapids near shore.	Intestines with wood fibers, 100.
5517	3. Pteronarcys californica..	July 5	Yellowstone R.	Rapids near shore.	Plant matter, 100.
5566J	3. Acroneuria pacifica.....	Aug. 10	Lost Creek....	Rapids of fair violence.	Heptagenia (2), 75; diatoms, 25.
5567a	1. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Drunella, 25; Heptagenia, 25; Rhyacophila, 45; wood fragments, 5.
5567a	2. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Tanytarsus pupa, 100. Gregarina.
5567a	3. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Tanytarsus larvae, 99; wood fragment, .5; pollen grain of pine, .5.
5567a	4. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Tanytarsus (5), 50; Heptagenia, 20; Rhyacophila, 28; detritus, 2.
5567a	5. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Tanytarsus (3), 50; Ephemerella, 49; Cladophora, 1.
5567a	6. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Chironomus in tube, 100.
5567a	7. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Empty.
5567a	8. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Detritus, 100.
5567a	9. Acroneuria pacifica.....	Aug. 11	Yellowstone R.	Strong rapids....	Tanytarsus, 100.
5567a	10. Pteronarcys californica..	Aug. 11	Yellowstone R.	Strong rapids....	Tanytarsus (3), 5; Cladophora, 75; shore diatoms, 15; wood and bark fragments, 5.
5567a	11. Pteronarcys californica..	Aug. 11	Yellowstone R.	Strong rapids....	Small moth, 100.
5567a	12. Pteronarcys californica..	Aug. 11	Yellowstone R.	Strong rapids....	Detritus, 100.
5572a	1. Perla verticalis ?	Aug. 12	Lost Creek...	Strong rapids....	Ephemerella, 40; Heptagenia, 50; Chironomus, 9; diatoms, 1.
5574d	1. Acroneuria pacifica......	Aug. 13	Lamar River..	Feeding among rocks in quiet current.	Chironomus larvae, 100. Gregarina.
5574d	2. Acroneuria pacifica.....	Aug. 13	Lamar River..	Feeding among rocks in quiet current.	Mayfly fragments, 100. Gregarina.
5574d	3. Acroneuria pacifica.....	Aug. 13	Lamar River..	Feeding among rocks in quiet current.	Tanytarsus (5), 20; mayfly nymph, 50; insect fragments, 20; detritus, 10. Gregarina.
5574d	4. Acroneuria pacifica.....	Aug. 13	Lamar River..	Feeding among rocks in quiet current.	Tanytarsus pupae (2), 100.
5574d	5. Acroneuria pacifica.....	Aug. 13	Lamar River..	Feeding among rocks in quiet current	Tanytarsus pupae (2), 90; wood fragments, 10. Gregarina.
5574d	6. Acroneuria pacifica.....	Aug. 13	Lamar River..	Feeding among rocks in quiet current.	Bachycentrus (2), 100.
5575a	1. Acroneuria pacifica.....	Aug. 14	Tower Creek..	Mild rapids......	Heptagenia, 60; Ephemerella, 20; Perla, 15; detritus, 5.
5575a	2. Acroneuria pacifica.....	Aug. 14	Tower Creek..	Mild rapids......	Ameletus (4), 100.
5575a	3. Acroneuria pacifica.....	Aug. 14	Tower Creek..	Mild rapids......	Heptagenia, 60; Rhyacophila (2), 40.
5575a	4. Acroneuria pacifica.....	Aug. 14	Tower Creek..	Mild rapids......	Chironomus pupa, 60; caddisworm, 40.
5575a	5. Acroneuria pacifica.....	Aug. 14	Tower Creek..	Mild rapids......	Chironomus (2), 40; Protenthes, 50; wood fragment, 10.
5585a	20. Acroneuria pacifica.....	Aug. 26	Lost Creek...	In shade. No vegetation.	Perla nymphs (5), 35; Chironomus pupa, 15; Melosira, 48; wood fragments, 2.
5585a	21. Acroneuria pacifica.....	Aug. 26	Lost Creek...	In shade. No vegetation.	Insect fragments, 15; Melosira, 85.

Table No. 1.—Showing the Food of the Perloidea or Stoneflies.—(*Continued*).

Collection Number	Number and Name of Individual Specimens	Date 1921	Locality	Habitat	Food Items in Percentages
5585a	22. Acroneuria pacifica.....	Aug. 26	Lost Creek...	In shade. No vegetation.	Chironomus, 5; Chironomus pupa, 20; perla nymphs (12), 65; Melosira, 5; detritus, 5.
5585a	23. Acroneuria pacifica.....	Aug. 26	Lost Creek...	In shade. No vegetation.	Insect fragments, 100.
5585a	24. Acroneuria pacifica.....	Aug. 26	Lost Creek...	In shade. No vegetation.	Cocconeis, 10; Melosira, 5; diatoms, 5; detritus, 80.
5585a	25. Acroneuria pacifica.....	Aug. 26	Lost Creek...	In shade. No vegetation.	Mayfly fragments, 30; Melosira, 5; detritus, 65.
5585b	20. Perla (verticalis).......	Aug. 25	Lost Creek...	Sunlit parts of stream.	Empty.
5585b	21. Perla (verticalis).......	Aug. 25	Lost Creek...	Sunlit parts of stream.	Heptagenia, 60; Chironomus pupa, 25; perla nymphs, 14; melosira, 1.
5585b	22. Perla (verticalis)........	Aug. 25	Lost Creek....	Sunlit parts of stream.	Perla nymphs (7), 99; Melosira, 1.
5585b	23. Perla (verticalis).......	Aug. 25	Lost Creek...	Sunlit parts of stream.	Perla nymphs (13), 100.
5585b	24. Perla (verticalis).......	Aug. 25	Lost Creek...	Sunlit parts of stream.	Chironomus pupa, 30; Melosira, 50; said, 10; wood fragments, 10; all in clearly marked zones in stomach.
5589a	12. Pteronarcys californi a..	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Moss, 60, bark, 35; diatoms, 5.
5589a	13. Pteronarcys californi.a..	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Moss, 80; Epithemia, 20.
5589a	14. Pteronarcys californi a..	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Moss, 50; diatoms, 10; Epithemia, 40.
5589a	15. Pteronarcys californica..	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Moss, 85; diatoms, 1; Epithemia, 14.
5589a	16. Pteronarcys californica..	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Moss, 50; diatoms, 10; Epithemia, 40.
5589a	17. Pteronarcys californica..	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Epithemia, 100. Small amount.
5589a	18. Acroneuria pacifica.....	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Ephemerella nymph, 99; moss, 1.
5589a	19. Acroneuria pacifica.....	Aug. 26	Lamar River..	Strong rapids among moss and Cladophora.	Insect fragments, 100.
5589b	8. Acroneuria pacifica.....	Aug. 26	Lamar River..	Minor rapids, among decaying Cladophora.	Chironomus larvae (16), 40; Perla, 40; sand, 20.
5589b	9. Acroneuria pacifica.....	Aug. 26	Lamar River..	Minor rapids, among decaying Cladophora.	Chironomus larvae (19), 95; sand, 5.
5589b	10. Acroneuria pacifica.....	Aug. 26	Lamar River..	Minor rapids, among decaying Cladophora.	Chironomus larvae (16), 90; Epithemia, 5; diatoms, 5.
5589b	11. Acroneuria pacifica.....	Aug. 26	Lamar River..	Minor rapids, among decaying Cladophora.	Chironomus larvae (6), 40; Perla nymphs, 50; insect fragments, 10.
5589b	12. Acroneuria pacifica.....	Aug. 26	Lamar River..	Minor rapids, among decaying Cladophora.	Perla numphs, 45; mayfly nymph fragments, 50; sand, 5.
5589b	13. Acroneuria pacifica.....	Aug. 26	Lamar River..	Minor rapids, among decaying Cladophora.	Chironomus larvae (2), 100.
5590a	1. Acroneuria pacifica.....	Aug. 26	Yellowstone R.	Moderate rapids.	Chironomus larvae (4), 40; Rhyacophila, 50; sand, 10. Gregarina.
5590a	2. Acroneuria pacifica.....	Aug. 26	Yellowstone R.	Moderate rapids..	Insect fragments, 100. Gregarina.
5590a	3. Acroneuria pacifica.....	Aug. 26	Yellowstone R.	Moderate rapids..	Rhyacophila, 100.
5590a	4. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Detritus, 100.
5590a	5. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Detritus, 100.
5590a	6. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Detritus, 100.
5590a	7. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Detritus, 100.
5590a	8. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Trebonema, 5; moss fragments, 10; detritus, 85.
5590a	9. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Trebonema, 15; moss fragments, 5; diatoms, 10; detritus, 70.

TABLE NO. 1.—SHOWING THE FOOD OF THE PERLOIDEA OR STONEFLIES.—(*Concluded*).

Collection Number	Number and Name of Individual Specimens	Date 1921	Locality	Habitat	Food Items in Percentages
5590a	10. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Bark fragments, 85; detritus, 15.
5590a	11. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Trebonema, 3; detritus, 97.
5590b	1. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Wood fragments, 85; detritus, 15.
5590b	2. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Detritus, 100.
5590b	3. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Sand, 5; diatoms, 5; detritus, 90.
5590b	4. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Wood fragments, 40; diatoms, 10; Trebonema, 5; detritus, 45.
5590b	5. Pteronarcys californica..	Aug. 26	Yellowstone R.	Moderate rapids..	Wood fragments, 3; diatoms, 5; Trebonema, 2; detritus, 90.
5590b	6. Acroneuria pacifica.....	Aug. 26	Yellowstone R.	Moderate rapids..	Insect fragments, 95; diatoms, 5.
5590b	7. Acroneuria pacifica.....	Aug. 26	Yellowstone R.	Moderate rapids..	Rhyacophila pupa (2), 100.
5590b	8. Acroneuria pacifica.....	Aug. 26	Yellowstone R.	Moderate rapids..	Chironomus (2), 90; sand, 10.
5590b	9. Acroneuria pacifica.....	Aug. 26	Yellowstone R.	Moderate rapids..	Empty.
5590c	1. Pteronarcys californica..	Aug. 26	Yellowstone R.	Strong, violent rapids.	Bark, 95; detritus, 5.
5590c	2. Pteronarcys californica..	Aug. 26	Yellowstone R.	Strong, violent rapids.	Bark, 25; detritus, 75.
5590c	3. Pteronarcys californica..	Aug. 26	Yellowstone R.	Strong, violent rapids.	Bark, 50; detritus, 50.
5590c	4. Pteronarcys californica..	Aug. 26	Yellowstone R.	Strong, violent rapids.	Empty.
5591a	7. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Minor rapids.....	Mayfly fragments, 100.
5591a	8. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Minor rapids.....	Detritus, 100.
5591a	9. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Minor rapids.....	Empty.
5591a	10. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Minor rapids.....	Detritus, 100.
5591a	11. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Minor rapids.....	Mayfly fragments, 95; detritus, 5.
5591a	12. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Minor rapids.....	Moth scales, 50; detritus, 50.
5591a	13. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Minor rapids.....	Chironomus larvae, 90; detritus, 10.
5591b	6. Acroneuria pacifica......	Aug. 27	Tower Creek..	Strong rapids....	Digested matter, 100.
5591b	7. Acroneuria pacifica.....	Aug. 27	Tower Creek..	Strong rapids....	Detritus, 100.
5591b	8. Alloperla sp...........	Aug. 27	Tower Creek..	Strong rapids....	Digested matter (plants?), 100.

TABLE NO. 2.—SHOWING SUMMARY OF FOOD OF PERLOIDEA. (EMPTY STOMACHS ARE NOT INCLUDED IN COMPUTING THE AVERAGES).

Name	Locality	Number of Specimens		Animal Food	Plant Food	Detritus
Pteronarcys........	Yellowstone River.......	20		5	43	52
Pteronarcys........	Lamar River...........	6		....	90	10
Average for	....	26	=	3.85	53.85	42.3
Acroneuria.........	Yellowstone River.......	14		90	1	9
Acroneuria.........	Lamar River...........	14		95.5	1.5	3
Acroneuria.........	Lost Creek............	7		50	30	20
Acroneuria.........	Tower Creek...........	14		60	5	35
Average for	....	49	=	77.4	6.3	16.3
Perla verticalis (?)	....	8		85	15	....

Undoubtedly, the stoneflies are the dominant insect forms of the mountain trout streams, particularly in Yellowstone and Lamar rivers. Previous to their final ecdysis, about the time the spring floods abate, the nymphs are extremely abundant and appear to constitute the bulk of the insect fauna. The stomachs of trout taken from the stream at this period are largely filled with stonefly nymphs.

But where are all these nymphs to obtain their food? They are carnivores, one generally reads. But if their numbers are so great that their bulk exceeds the available animal food supply, how can they subsist? This was one of the puzzles the senior author met early in the work,—one which was not solved until the present data were obtained.

From the examination of the stomach contents of Perlid nymphs several surprising results were obtained: (1) That Perloidea are not exclusively carnivores, but that their diet contains an admixture of plant matter and detritus, i. e., predigested and decomposed matter. (2) That the largest species, *Pteronarcys californica*, is largely a vegetarian. (3) That about 12% of those Perloidea whose main diet was animal matter, were parasitized by gregarines.

The diet of *Pteronarcys* was perhaps the most surprising result. It's first notice was so unexpected that thereafter special efforts were made to secure a considerable number of specimens from different localities for examination. Whether this species is really a vegetarian, or whether it is so only on occasion, cannot be stated positively. Only this much seems clear: The specimens examined, about thirty in number, had fed chiefly on a plant diet, averaging less than 4% animal diet.

The other prominent perlid species, *Acroneuria pacifica*, is quite evidently a carnivore. The admixture of plant food and detritus may be accounted for on the basis that they were taken in with the insect food. It is also possible, that the gregarines found in six of the *Acroneuria* were not "resident" parasites, but were taken in with some insect hosts, such as mayfly nymphs or caddisworms.

In a very interesting study of *Nemoura*, C. F. Wu ('23, p. 39) remarks as follows: "Besides some fine sediment and the half digested fragments of decaying leaves, there were found great varieties of unicellular algae, chiefly diatoms and desmids. No remains of animal tissue have ever been detected, so that naiads are herbivorous in their food habits." Relative to the food of the adult Wu (l. c.) states, "Of the various kinds of living plant leaves found around the water and fed to the adults, the young leaves of Touch-me-not are eaten." Newcomer ('18) reports the adults of *Taeniopteryx pacifica* as feeding on the buds and leaves of plants and causing considerable injury.

Food of Ephemeroidea or Mayfly Nymphs. The following table shows in detail the food percentages of the mayfly nymphs examined.

TABLE NO. 3.—SHOWING FOOD OF MAYFLY NYMPHS.

Collection Number	Number and Name of Individual Specimens	Date, 1921	Locality	Habitat	Food Items in Percentages
5566b	3. Ameletus	Aug. 10	Lost Creek	From rocks with clusters of vegetation, chiefly Melosira and some Gomphonema and Closterium.	Melosira, 90; Gomphonema, 10.
5566b	1. Drunella sp	Aug. 10	Lost Creek	Pure Melosira	Melosira, 99; Gomphonema, .5; protozoan, .5.
5566b	2. Drunella sp	Aug. 10	Lost Creek	....	Melosira, 99; Gomphonema, 1.
5566d	1. Drunella sp	Aug. 10	Lost Creek	From Prasiola and Oscillatoria.	Melosira, 80; Closterium, 1; Oscillatoria, 19.
5566d	2. Drunella sp	Aug. 10	Lost Creek	From Prasiola and Oscillatoria.	Prasiola, 99; Oscillatoria, 1.
5566d	5. Ephemerella sp	Aug. 10	Lost Creek	From Prasiola and Oscillatoria.	Melosira, 50; empty diatom shells, 50.
5566d	6. Ephemerella sp	Aug. 10	Lost Creek	From Prasiola and Oscillatoria.	Prasiola, 100.
5566j	1. Heptagenia sp	Aug. 10	Lost Creek	From Prasiola	Melosira, 60; Oscillatoria, 40.
5566h	4. Ephemerella sp	Aug. 10	Lost Creek	From barren region	Empty.
5566i	1. Ephemerella sp	Aug. 10	Lost Creek	Barren region with few diatom shells.	Melosira, 75; mixed diatoms, 25.
5566i	2. Ephemerella sp	Aug. 10	Lost Creek	Barren region with few diatom shells.	Melosira, 95; mixed diatoms, 5.
5566j	2. Heptagenia sp	Aug. 10	Lost Creek	Barren, with few diatoms.	Melosira, 50; Oscillatoria, 45; diatoms, 5.
5566j	7. Ephemerella sp	Aug. 10	Lost Creek	Barren, with few diatoms.	Prasiola, 99; Oscillatoria, 1.
5566j	8. Ephemerella sp	Aug. 10	Lost Creek	Barren, with few diatoms.	Gomphonema, 85; diatoms, 15.
5566k	1. Heptagenia sp	Aug. 10	Lost Creek	Barren with few diatoms, some Closterium.	Melosira, 85; diatoms and Closterium, 15.
5566k	2. Ameletus sp	Aug. 10	Lost Creek	Barren with few diatoms, some Closterium.	Melosira, 100.
5566l	1. Ephemerella sp	Aug. 10	Lost Creek	Mostly Oscillatoria. Traces of Melosira.	Oscillatoria, 99; diatoms, 1.
5566l	2. Ephemerella sp	Aug. 10	Lost Creek	Mostly Oscillatoria. Traces of Melosira.	Oscillatoria, 99; diatoms, 1.
5567a	15. Ameletus sp	Aug. 11	Yellowstone R.	Strong rapids	Sand, 95; diatoms, 5.
5567a	16 19. Ameletus sp	Aug. 11	Yellowstone R.	Strong rapids	Detritus, 100.
5567a	20. Ameletus sp	Aug. 11	Yellowstone R.	Strong rapids	Fresh diatoms, 15; sand, 85.
5567a	21, 22. Ameletus sp	Aug. 11	Yellowstone R.	Strong rapids	Both with detritus, 100.
5567a	23. Heptagenia sp	Aug. 11	Yellowstone R.	Strong rapids	Detritus, 100.
5567a	24. Heptagenia sp	Aug. 11	Yellowstone R.	Strong rapids	Sand, 50; diatoms, 5; detritus, 45.
5567a	25. Heptagenia sp	Aug. 11	Yellowstone R.	Strong rapids	Detritus, 100.
5567a	26. Heptagenia sp	Aug. 11	Yellowstone R.	Strong rapids	Sand, 15; diatoms, 5; detritus, 80.
5567a	27. Heptagenia sp	Aug. 11	Yellowstone R.	Strong rapids	Sand, 5; diatoms, 5; detritus, 90.
5567a	28. Heptagenia sp	Aug. 11	Yellowstone R.	Strong rapids	Diatoms, 5; detritus, 95.
5567a	29. Ephemerella sp	Aug. 11	Yellowstone R.	Strong rapids	Cladophora, 5; sand, 10; detritus, 85.
5567a	30, 31. Ephemerella sp.	Aug. 11	Yellowstone R.	Strong rapids	Both with detritus, 100.
5567a	32. Ephemerella sp	Aug. 11	Yellowstone R.	Strong rapids	Detritus, 75; adult dipteran, 25.
5567a	33, 34. Ephemerella sp.	Aug. 11	Yellowstone R.	Strong rapids	Both with detritus, 100.
5572a	4. Ameletus sp	Aug. 12	Lost Creek	Rapids. Vegetation: Melosira, Prasiola, Oscillatoria, Calpoda and Rotifera among plants.	Melosira, 50; detritus, 50.
5572a	5, 6. Ameletus sp	Aug. 12	Lost Creek	Rapids. Vegetation: Melosira, Prasiola, Oscillatoria, Calpoda and Rotifera among plants.	Both with detritus, 100.
5572a	7. Heptagenia sp	Aug. 12	Lost Creek	Rapids. Vegetation: Melosira, Prasiola, Oscillatoria, Calpoda and Rotifera among plants.	Rock diatoms, 15; sand, 5; detritus, 80.
5572b	5. Ameletus sp	Aug. 12	Lost Creek	Among rocks in rapids. Much detritus and Melosira.	Melosira, 50; detritus, 50.
5572b	6. Ameletus sp	Aug. 12	Lost Creek	Among rocks in rapids. Much detritus and Melosira.	Detritus, 50; sand, 25; rock diatoms, 25.
5572b	7. Ameletus sp	Aug. 12	Lost Creek	Among rocks in rapids. Much detritus and Melosira.	Rock diatoms, 75; detritus, 20; sand, 5.
5572b	8. Ephemerella sp	Aug. 12	Lost Creek	Among rocks in rapids. Much detritus and Melosira.	Rock diatoms, 85; detritus, 5; diatoms, 10.
5572b	9. Ephemerella sp	Aug. 12	Lost Creek	Among rocks in rapids. Much detritus and Melosira.	Rock diatoms, 75; detritus, 23; sand, 2.

TABLE No. 3.—SHOWING FOOD OF MAYFLY NYMPHS.—(*Continued*).

Collection Number	Number and Name of Individual Specimens	Date, 1921	Locality	Habitat	Food Items in Percentages
5572b	10. Drunella sp......	Aug. 12	Lost Creek....	Among rocks in rapids. Much detritus and Melosira.	Wood fibers, 35; detritus, 65.
5572e	1. Heptagenia sp....	Aug. 12	Lost Creek....	From rocks in rapids. Moss and Prasiola. Melosira caught in moss.	Detritus, 95; wood fragments, 2; mixed diatoms, 3.
5572e	2, 3, 4. Heptagenia sp.	Aug. 12	Lost Creek....	From rocks in rapids. Moss and Prasiola. Melosira caught in moss.	All with detritus, 100.
5572e	5. Heptagenia sp....	Aug. 12	Lost Creek....	From rocks in rapids. Moss and Prasiola. Melosira caught in moss.	Detritus, 95; mixed diatoms, 5.
5575b	1. Baetis sp........	Aug. 14	Tower Creek...	Mild rapids............	Sand, 20; detritus, 80.
5575b	2. Baetis sp........	Aug. 14	Tower Creek...	Mild rapids............	Detritus, 100.
5575c	1. Ephemerella sp...	Aug. 14	Tower Creek...	From lateral rapids......	Sand, 20; detritus, 80.
5575c	2. Ephemerella sp...	Aug. 14	Tower Creek...	From lateral rapids......	Sand, 10; detritus, 50; wood fragments, 15; insect fragments, 25.
5575c	3, 4. Ephemerella sp.	Aug. 14	Tower Creek...	From lateral rapids......	Detritus, 100.
5575d	1. Ameletus sp.....	Aug. 14	Tower Creek...	Mild rapids............	Diatoms, 1; wood fragments, 4; detritus, 75; sand, 20.
5575e	1. Ephemerella sp...	Aug. 14	Tower Creek...	From lesser rapids.......	Heptagenia, 50; detritus, 49; wood, 1.
5584a	15. Heptagenia sp....	Aug. 25	Lost Creek.....	Shaded area. No vegetation.	Detritus, 30; Cocconeis, 65; wood fragments, 2; mixed fragments, 3.
5584a	16. Heptagenia sp....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Cocconeis, 25; Rhoicosphenia, 25; mixed diatoms, 5; detritus, 40; sand, 5.
5584a	17. Drunella sp......	Aug. 25	Lost Creek....	Shaded areas. No vegetation.	Cocconeis, 40; Rhoicosphenia, 5; mixed diatoms, 5; detritus, 50.
5584a	18. Drunella sp......	Aug. 25	Lost Creek....	Shaded areas. No vegetation.	Cocconeis, 35; Melosira, 15; Synedra, 3; mixed diatoms, 7; sand, 5; detritus, 35.
5584a	19. Drunella sp......	Aug. 25	Lost Creek....	Shaded areas. No vegetation.	Sand, 25; Cocconeis, 25; Melosira, 5; mixed diatoms, 5; detritus, 40.
5589a	20. Drunella sp......	Aug. 26	Lamar River...	Strong rapids. Feeding on moss and Cladophora.	Epithemia, 80; Cocconeis, 10; mixed diatoms, 10.
5589a	21. Drunella sp......	Aug. 26	Lamar River...	Strong rapids. Feeding on moss and Cladophora.	Epithemia, 50; detritus, 50.
5589b	14. Ephemerella sp...	Aug. 26	Lamar River...	Minor rapids. Feeding among decaying Cladophora.	Chironomus (2), 5; Epithemia, 50; mixed diatoms, 10; detritus, 35.
5589b	15. Ephemerella sp...	Aug. 26	Lamar River...	Minor rapids. Feeding among decaying Cladophora.	Sand, 5; Epithemia, 50; mixed diatoms, 10; detritus, 35.
5589b	16. Ephemerella sp...	Aug. 26	Lamar River...	Minor rapids. Feeding among decaying Cladophora.	Sand, 5; Epithemia, 15; diatoms, 10; detritus, 70.
5589b	17. Ephemerella sp...	Aug. 26	Lamar River...	Minor rapids. Feeding among decaying Cladophora.	Mixed diatoms, 5; detritus, 95.
5589b	18. Ameletus sp.....	Aug. 26	Lamar River...	Minor rapids. Feeding among decaying Cladophora.	Epithemia, 75; diatoms, 10; detritus, 15.
5589b	19, 20. Ameletus sp..	Aug. 26	Lamar River...	Minor rapids. Feeding among decaying Cladophora.	Both with Epithemia, 10; diatoms, 15; detritus, 75.
5590a	13. Heptagenia sp....	Aug. 26	Yellowstone R.	Moderate rapids.........	Cladophora, 90; sand, 10.
5590a	14. Heptagenia sp....	Aug. 26	Yellowstone R.	Moderate rapids.........	Detritus, 100.
5590b	9. Ephemerella sp...	Aug. 26	Yellowstone R.	Minor rapids............	Detritus, 100.
5590b	10. Ephemerella sp...	Aug. 26	Yellowstone R.	Minor rapids............	Detritus, 85; diatoms, 5; Trebonema, 10.
5590b	11. Ephemerella sp...	Aug. 26	Yellowstone R.	Minor rapids............	Detritus, 90; diatoms, 5; Trebonema, 5.
5591a	14. Heptagenia sp....	Aug. 27	Tower Creek...	Minor rapids............	Detritus, 100.
5591a	15. Heptagenia sp....	Aug. 27	Tower Creek...	Minor rapids............	Detritus, 99; diatoms, 1.
5591a	16, 17, 18. Heptagenia sp.	Aug. 27	Tower Creek...	Minor rapids............	All with detritus, 100.
5591a	19. Ameletus sp.....	Aug. 27	Tower Creek...	Minor rapids............	Sand, 15; detritus, 85.
5591a	20. Ameletus sp.....	Aug. 27	Tower Creek...	Minor rapids............	Sand, 18; detritus, 80; diatoms, 2.
5591a	21. Ephemerella sp...	Aug. 27	Tower Creek...	Minor rapids............	Sand, 1; detritus, 97; diatoms, 2.
5591a	22. Ephemerella sp...	Aug. 27	Tower Creek...	Minor rapids............	Sand, 1; detritus, 97; diatoms, 2.
5591a	23. Drunella sp......	Aug. 27	Tower Creek...	Minor rapids............	Insect fragments, 50; wood fragments, 45; detritus, 5. Gregarina as parasites.

TABLE NO. 3.—SHOWING FOOD OF MAYFLY NYMPHS.—*(Concluded)*.

Collection Number	Number and Name of Individual Specimens	Date, 1921	Locality	Habitat	Food Items in Percentages
5591a	24. Drunella sp......	Aug. 27	Tower Creek...	Minor rapids............	Wood fragments, 10; detritus, 90. Gregarina.
5591a	25. Drunella sp......	Aug. 27	Tower Creek...	Minor rapids...........	Insect fragments, 80; diatoms, 2; detritus, 18. Gregarina.
5591a	26. Drunella sp......	Aug. 27	Tower Creek...	Minor rapids............	Detritus, 100. Gregarina.
5591a	27. Drunella sp......	Aug. 27	Tower Creek...	Minor rapids............	Insect fragments, 5; wood fragments, 10; sand, 4; diatoms, 1; detritus, 80.
5591a	28. Heptagenia sp....	Aug. 27	Tower Creek...	Minor rapids............	Diatoms, 20; detritus, 70; sand, 10. With nematode (Mermis sp.?) as parasite.
5591a	29. Heptagenia sp....	Aug. 27	Tower Creek...	Minor rapids............	Diatoms, 20; detritus, 70; sand, 10. With two nematode parasites (Mermis sp.?).
5591b	9. Ameletus sp......	Aug. 27	Tower Creek...	Strong rapids...........	Detritus, 100.
5591b	10. Ameletus sp.....	Aug. 27	Tower Creek...	Strong rapids...........	Detritus, 95; diatoms, 5.
5591b	11. Ameletus sp.....	Aug. 27	Tower Creek...	Strong rapids...........	Detritus, 94; sand, 5; diatoms, 1.
5591b	12. Drunella sp......	Aug. 27	Tower Creek...	Strong rapids...........	Insect fragments, 75; sand, 5; detritus, 20. With gregarina.
5591b	13. Drunella sp......	Aug. 27	Tower Creek...	Strong rapids...........	Insect fragments, 10; sand, 5; detritus, 85. Gregarina.
5591b	14. Drunella sp......	Aug. 27	Tower Creek...	Strong rapids...........	Bark fragments, 20; sand, 5; detritus, 75. Gregarina.
5591b	15. Drunella sp......	Aug. 27	Tower Creek...	Strong rapids...........	Diatoms, 2; sand, 23; detritus, 75. Gregarina.
5591b	16. Heptagenia sp....	Aug. 27	Tower Creek...	Strong rapids...........	Detritus, 100.
5591b	17. Heptagenia sp....	Aug. 27	Tower Creek...	Strong rapids...........	Diatoms, 5; sand, 5; detritus, 90.
5591b	18. Heptagenia sp....	Aug. 27	Tower Creek...	Strong rapids...........	Sand, 5; detritus, 95.
5591e	2. Heptagenia sp....	Aug. 27	Tower Creek...	Lateral pools. With moderate current.	Detritus, 100.
5591e	3, 4. Heptagenia sp..	Aug. 27	Tower Creek...	Lateral pools. With moderate current.	Both with detritus, 100.
5591e	5. Drunella sp......	Aug. 27	Tower Creek...	Lateral pools. With moderate current.	Insect fragments, 100. Gregarina.
5591e	6. Drunella sp......	Aug. 27	Tower Creek...	Lateral pools. With moderate current.	Insect fragments, 50; wood fragments, 20; detritus, 30. Gregarina.

TABLE NO. 4.—SHOWING SUMMARY OF FOOD OF MAYFLY NYMPHS.

Name	Locality	Number of Specimens	Animal Food	Plant Food	Detritus
Ameletus sp.	Yellowstone R.	8	....	2	98
Ameletus sp.	Lamar River	3	....	45	55
Ameletus sp.	Lost Creek	8	....	50	50
Ameletus sp.	Tower Creek	6	....	3	97
Average for		25 =		22.7	77.3
Drunella sp.	Lamar River	2	....	75	25
Drunella sp.	Lost Creek	7	....	68	32
Drunella sp.	Tower Creek	11	33.6	10	56.4
Average for		20 =	18.5	36.8	44.7
Baetis sp.	Tower Creek	2	....	50	50
Ephemerella sp.	Yellowstone R.	9	2.6	3.4	94
Ephemerella sp.	Lamar River	4	1.25	37	61.75
Ephemerella sp.	Lost Creek	8	....	96.25	3.75
Ephemerella sp.	Tower Creek	7	11	10	79
Average for		28 =	3.7	36.3	60
Heptagenia sp.	Yellowstone R.	8	....	14	86
Heptagenia sp.	Lost Creek	13	....	50	50
Heptagenia sp.	Tower Creek	13	....	4	96
Average for		34 =		24	76

From the predominance of detritus in the food of mayfly nymphs, as indicated by the averages, it would seem that these nymphs are primarily scavengers. They appear to feed on the flotsam and jetsam that is caught between rocks, on diatoms, and the bits of filamentous algae that grow on rocks. The animal matter eaten may possibly be dead specimens caught with the flotsam.

Of *Drunella* ten specimens, and these all from Tower Creek, were parasitized by gregarines. Two *Heptagenia* are noted as parasitized by a nematode, perhaps a species of *Mermis;* these, too, were taken from Tower Creek. In another paper (Muttkowski, '25, Fig. 124, facing p. 485) is shown an adult mayfly with such a nematode emerging from the caudal end. This adult was taken from Gardiner River, at its junction with Lava Creek, a short distance from Mammoth Hot Springs.

Whether these records indicate that only *Drunella* is parasitized by *Gregarina,* and *Heptagenia* by a nematode parasite, is conjectural. The records are too few to permit any definite conclusions.

The proportions of plant and animal matter and of unidentifiable detritus accord well with the findings of Needham ('20) for midwestern lakes and streams.

The Food of Trichoptera. The following table shows in detail the food percentages of the specimens of caddisworms studied.

Table No. 5.—Showing Food of Trichoptera.

Collection Number	Specimen Number and Name	Date, 1921	Locality	Habitat	Food in Percentages
5566a	1. Rhyacophila	Aug. 10	Lost Creek	Rocks splashed with spray	Rotifera, 60; Oscillatoria, 40.
5566h	1. Thremma	Aug. 10	Lost Creek	Vegetation consisting of Melosira, chiefly. Some Gomphonema and Closterium.	Melosira, 99; Colpoda, 1.
5566d	3. Thremma	Aug. 10	Lost Creek	From Prasiola and Oscillatoria.	Melosira, 100.
5566d	4. Thremma	Aug. 10	Lost Creek	....	Empty.
5566d	1. Hydropsyche	Aug. 10	Lost Creek	From shady area	Spirogyra, 50; empty diatom shells, 50.
5566d	2. Hydropsyche	Aug. 10	Lost Creek	From shady area	Melosira, 80; diatom shells, 17; Closterium, 3.
5566d	3. Hydropsyche	Aug. 10	Lost Creek	From shady area	Diatom shells, 100.
5566d	5. Thremma pupa	Aug. 10	Lost Creek	From shady area	Empty.
5566i	3. Hydropsyche	Aug. 10	Lost Creek	Prasiola and diatoms	Melosira, 95; mixed diatoms, 5.
5566i	4. Hydropsyche	Aug. 10	Lost Creek	Prasiola and diatoms	Melosira, 65; mixed diatoms, 35.
5566i	5. Rhyacophila	Aug. 10	Lost Creek	Prasiola and diatoms	Diatom shells, 100. Gregarine parasites.
5566j	1. Rhyacophila	Aug. 10	Lost Creek	Barrens. Few diatom shells.	Rotifers, 1; chironomids, 4; Melosira, 40; diatoms, 10; Oscillatoria, 45.
5566j	2. Hydropsyche	Aug. 10	Lost Creek	Barrens. Few diatom shells.	Mayfly, 1; ad. Chironomus, 90; Melosira, 5; diatoms, 4.
5566j	6. Rhyacophila	Aug. 10	Lost Creek	Barrens. Few diatom shells.	Mayfly nymph, 30; Chironomus ad., 60; Melosira, 5; diatoms, 5; Gregarina.
5566l	3. Rhyacophila	Aug. 10	Lost Creek	Oscillatoria with trace of Melosira.	Oscillatoria, 95; diatoms, 5.
5566l	4. Rhyacophila	Aug. 10	Lost Creek	Oscillatoria with trace of Melosira.	Caddisworm, 30; Chironomus ad., 30; diatoms, 10; Oscillatoria, 30.
5566l	5. Hydropsyche	Aug. 10	Lost Creek	Oscillatoria with trace of Melosira.	Mayfly nymphs (5), 30; Chironomus larvae (10), 50; Melosira, 15; Oscillatoria, 5.
5587a	35. Hydropsyche	Aug. 11	Yellowstone R.	Rapids	Chironomus, 10; stem parenchyma, 15; diatoms (Melosira chiefly), 15; detritus, 60.
5587a	36. Hydropsyche	Aug. 11	Yellowstone R.	Rapids	Mayfly nymph, 95; sand, 5.
5587a	40. Brachycentrus	Aug. 11	Yellowstone R.	Rapids	Wood fragments, 50; diatoms, 15; detritus, 35.
5587a	48. Hydropsyche	Aug. 11	Yellowstone R.	Rapids	Tanypus pupa, 40; shore diatoms, 20; lake plankton, 5; Rhizoclonium, 5; detritus, 30.
5587a	49. Philopotamus?	Aug. 11	Yellowstone R.	Rapids	Empty.
5587a	50. Thremma	Aug. 11	Yellowstone R.	Rapids	Shore diatoms, 50; Tritonema, 5; detritus, 45.
5572a	2. Hydropsyche	Aug. 12	Lost Creek	Rapids. Oscillatoria, Prasiola, and Melosira. Colpoda and rotifers feeding among plants.	Ameletus, 25; Ephemerella, 35; Melosira, 40.
5572a	3. Hydropsyche	Aug. 12	Lost Creek	....	Glossosoma (?) pupae (3), 40; Glossosoma (?) larvae, 10; Ephemerella, 15; Chironomus adult, 25; Melosira, 20.
5572b	1. Hydropsyche	Aug. 12	Lost Creek	Rocks in rapids. Accumulations of detritus and Melosira. Ameba and Colpoda feeding.	Ephemerella (5), 50; Glossosoma (?), pupa, 35; Melosira, 10; detritus, 5. Gregarina.
5572b	2. Hydropsyche	Aug. 12	Lost Creek	Rocks in rapids. Accumulations of detritus and Melosira. Ameba and Colpoda feeding.	Chironomus (2), 20; caddisflies (6), 65; Melosira, 14; sand and detritus, 1.
5572b	3. Hydropsyche	Aug. 12	Lost Creek	Rocks in rapids. Accumulations of detritus and Melosira. Ameba and Colpoda feeding.	Chironomus (2), 50; Chironomus adult, 45; Melosira, 3; detritus, 2. Gregarina.
5572b	4. Hydropsyche	Aug. 12	Lost Creek	Rocks in rapids. Accumulations of detritus and Melosira. Ameba and Colpoda feeding.	Caddisflies (7), 75; Acroneuria sp. leg, 7; wood fragment, 10; trichopterous pupa, 5; Melosira, 3. Gregarina
5574a	1. Brachycentrus	Aug. 13	Lamar River	Rapids	Trebonema, 20; Cymbella, 40; Cocconeis, 20; Synedra, 10; diatoms, 10; Gregarina.

TABLE NO. 5.—SHOWING FOOD OF TRICHOPTERA.—(*Continued*).

Collection Number	Specimen Number and Name	Date, 1921	Locality	Habitat	Food in Percentages
5574a	2. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Tanytarsus, 2[illegible]; Nauplii (?), 30; wood fibers, 50. Gregarina.
5574a	3. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Chironomus, 5; mayfly nymph, 20; Cocconeis, 50; Synedra, 20; minor diatoms, 5. Gregarina.
5574a	4. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Tanytarsus pupa, 30; Cocconeis, 30; Synedra, 30; minor diatoms, 10. Gregarina.
5574a	5. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Mayfly fragments, 20; Trebonema, 5; Cocconeis, 65; Melosira, 5; minor diatoms, 5. Gregarina.
5574a	6. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Synedra, 50; mixed diatoms, 10; detritus, 40. Gregarina.
5574a	7. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Tanytarsus, 25; Cladophora, 20; diatoms, 10; detritus, 55. Gregarina.
5574a	8. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Mayfly fragments, 30; Melosira, 20; Cladophora, 20; diatoms, 10; detritus, 20. Gregarina.
5574a	9. Brachycentrus....	Aug. 13	Lamar River...	Rapids.................	Mayfly fragments, 10; Cocconeis, 5; Melosira, 65; diatoms, 10; detritus, 10. Gregarina.
5574b	1. Brachycentrus sp.	Aug. 13	Lamar River...	Violent rapids...........	Tanytarsus pupae, 80; plant tissues, 15; diatoms, 5. Gregarina.
5574b	2. Brachycentrus sp.	Aug. 13	Lamar River...	Violent rapids...........	Synedra, 5; detritus, 95. Gregarina.
5574b	3. Brachycentrus sp.	Aug. 13	Lamar River...	Violent rapids...........	Mayfly fragments, 10; diatoms, 1; detritus, 89. Gregarina.
5574b	4. Brachycentrus sp.	Aug. 13	Lamar River...	Violent rapids...........	Mayfly fragments, 20; Synedra, 60; Cocconeis, 10; detritus, 10. Gregarina.
5574b	5. Brachycentrus sp.	Aug. 13	Lamar River...	Violent rapids...........	Tanytarsus larvae, 5; Tanytarsus purpae, 15; Synedra, 10; Cocconeis, 10; detritus, 60. Gregarina.
5574c	1. Brachycentrus sp.	Aug. 13	Lamar River...	From Cladophora.......	Tanytarsus pupae, 30; Cladophora, 40; Cocconeis, 25; diatoms, 5. Gregarina.
5574c	2. Brachycentrus sp.	Aug. 13	Lamar River...	From Cladophora.......	Detritus, 5; Cladophora, 70; Cocconeis, 20; diatoms, 5. Gregarina.
5574c	3. Brachycentrus sp.	Aug. 13	Lamar River...	From Cladophora........	Cladophora, 85; Cocconeis, 14; diatoms, 1. Gregarina.
5574c	4. Brachycentrus sp.	Aug. 13	Lamar River...	From Cladophora.......	Synedra, 5; Cladophora, 30; Cocconeis, 60; diatoms, 5. Gregarina.
5574c	5. Brachycentrus sp.	Aug. 13	Lamar River...	From Cladophora.......	Cladophora, 85; Cocconeis, 14; diatoms, 1. Gregarina.
5574c	6. Brachycentrus sp.	Aug. 13	Lamar River...	From Cladophora.......	Synedra, 4; Cladophora, 20; Cocconeis, 75; diatoms, 1. Gregarina.
5575f	1. Thremma........	Aug. 14	Tower Creek...	Rapids.................	Cocconeis, 5; detritus, 95.
5575f	2. Thremma........	Aug. 14	Tower Creek...	Rapids.................	Detritus, 100.
5575g	1. Rhyacophila.....	Aug. 14	Tower Creek...	Lateral pools...........	Rhyacophila (3), 80; detritus, 20. Gregarina.
5575g	2. Rhyacophila.....	Aug. 14	Tower Creek...	Lateral pools...........	Glossosoma (?) pupa, 90; detritus, 10. Gregarina.
5575g	3. Rhyacophila.....	Aug. 14	Tower Creek...	Lateral pools...........	Chironomus, 20; mayfly caudal setae, 80.
5585a	1. Hydropsyche.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Chironomus (3), 10; mayfly nymph, 10; Melosira, 75; diatoms, 5. Gregarina.
5585a	2. Hydropsyche.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Mayfly fragments, 10; Melosira, 85; diatoms, 5. Gregarina.
5585a	3. Hydropsyche.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Chironomus, 2; mayfly fragments, 18; Melosira, 75; diatoms, 5. Gregarina.

TABLE No. 5.—SHOWING FOOD OF TRICHOPTERA.—(*Continued*).

Collection Number	Specimen Number and Name	Date, 1921	Locality	Habitat	Food in Percentages
5585a	4. Hydropsyche.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Chironomus, 5; mayfly fragments, 10; Glossosoma (?) pupae, 20; Hydrachnid, 3; Melosira, 60; diatoms, 2. Gregarina.
5585a	5. Hydropsyche.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Melosira, 18; diatoms, 2; Glossosoma (?) pupa, 40; mayfly fragments, 40. Gregarina.
5585a	6. Rhyacophila.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Empty. Gregarina.
5585a	7. Rhyacophila.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Mayfly fragments, 50; Melosira, 25; wood fragments, 20; diatoms, 5. Gregarina.
5585a	8. Rhyacophila.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Insect fragments, 100. Gregarina.
5585a	9. Rhyacophila.....	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Glossosoma (?) pupa, 50; wood fragments, 49; Melosira, 1. Gregarina.
5585a	10. Glossosoma (?)...	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Rhoicosphenia, 96; Cocconeis, 3; diatoms, 1. Gregarina.
5585a	11. Glossosoma (?)...	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Rhoicosphenia, 92; Cocconeis, 8. Gregarina.
5585a	12. Glossosoma (?)...	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Empty.
5585a	13. Glossosoma (?)...	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Rhoicosphenia, 90; Cocconeis, 4; wood fragments, 4; mixed diatoms, 2. Gregarina.
5585a	14. Glossosoma (?)...	Aug. 25	Lost Creek....	Shaded area. No vegetation.	Melosira, 95; Cocconeis, 2; Synedra, 2; other diatoms, 1. Gregarina.
5585b	1. Hydropsyche.....	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Mayfly fragments, 25; Glossosoma (?) pupa, 25; Melosira, 50. Gregarina.
5585b	2. Hydropsyche.....	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Mayfly fragments, 5; Synedra, 5; Melosira, 90. Gregarina.
5585b	3. Hydropsyche.....	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Mayfly fragments, 15; diatoms, 2; Melosira, 83. Gregarina.
5585b	4. Hydropsyche.....	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Mayfly fragments, 15; Glossosoma (?) pupa, 15; Melosira, 68; diatoms, 2. Gregarina.
5585b	5. Hydropsyche.....	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Mayfly fragments, 40; Chironomus pupa, 5; Perlid young (2), 15; Melosira, 38; mixed diatoms, 2; Gregarina.
5585b	6. Rhyacophila sp...	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Rhyacophila, 50; perlid young, 10; mayfly fragments, 25; Melosira, 15.
5585b	7. Rhyacophila sp...	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Mayfly fragments, 100. Gregarina.
5585b	8. Rhyacophila sp...	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Perlid young (3), 60; insect fragments, 40. Gregarina.
5585b	9. Rhyacopnila sp...	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Mayfly fragments, 99; Melosira, 1. Gregarina.
5585b	10. Rhyacophila sp...	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Melosira (small amount), 100. Gregarina.
5585b	11. Thremma........	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Melosira, 50; Cocconeis, 5; diatoms, 5; detritus, 40.

TABLE NO. 5.—SHOWING FOOD OF TRICHOPTERA.—(*Continued*).

Collection Number	Specimen Number and Name	Date, 1921	Locality	Habitat	Food in Percentages
5585b	12. Thremma........	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Rhoicosphenia, 10; Cocconeis, 35; Melosira, 10; diatoms, 5; detritus, 40.
5585b	13. Thremma........	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Cocconeis, 50; Melosira, 30; diatoms, 5; detritus, 15.
5585b	14. Thremma........	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Rhoicosphenia, 5; Cocconeis, 10; Melosira, 10; diatoms, 5; detritus, 70.
5585b	15. Thremma........	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Rhoicosphenia, 65; Cocconeis, 15; diatoms, 5; detritus, 15.
5585b	16. Thremma........	Aug. 25	Lost Creek....	Sunlit areas. Melosira predominant. Some Oscillatoria and Prasiola.	Cocconeis, 5; diatoms, 5; detritus, 90.
5589a	1. Brachycentrus....	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Moss, 90; Cymbella, 10. Gregarina.
5589a	2. Brachycentrus....	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Chironomus pupae (4), 40; Chironomus larva, 5; mayfly nymph, 30; Cladophora, 10; Cocconeis, 10; Cymbella, 3; diatoms, 2. Gregarina.
5589a	3. Brachycentrus....	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Trebonema, 50; Cladophora, 10; Cocconeis, 35; diatoms, 5. Gregarina.
5589a	4. Brachycentrus....	Aug. 26	Lamar River..	Strong rapids. From moss and Cladophora.	Chironomus, 15; Cladophora, 5; Cocconeis, 5; diatoms, 5; mayfly fragments, 30; moss fragments, 30; Epithemia, 10. Gregarina.
5589a	5. Brachycentrus....	Aug. 26	Lamar River...	Stong rapids. From moss and Cladophora.	Moss, 40; Trebonema, 30; Epithemia, 15; Cocconeis, 5; Cladophora, 5; diatoms, 5. Gregarina.
5589a	6. Brachycentrus....	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Mayfly fragments, 10; Cocconeis, 30; Chironomus, 5; diatoms, 5; Epithemia, 50. Gregarina.
5589a	7. Brachycentrus....	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Cocconeis, 14; diatoms, 1; Epithemia, 85. Gregarina.
5589a	8. Thremma........	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Moss, 70; Epithemia, 30.
5589a	9. Thremma........	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Moss, 70; Epithemia, 30.
5589a	10. Thremma........	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Moss, 70; Epithemia, 30.
5589a	11. Thremma........	Aug. 26	Lamar River...	Strong rapids. From moss and Cladophora.	Moss, 70; Epithemia, 30.
5589b	1. Brachycentrus....	Aug. 26	Lamar River...	Minor rapids. Decaying Cladophora.	Mayfly fragments, 50; Melosira, 35; Cocconeis, 5; Epithemia, 5; diatoms, 5. Gregarina.
5589b	2. Brachycentrus....	Aug. 26	Lamar River...	Minor rapids. Decaying Cladophora.	Mayfly fragments, 30; Chironomus, 5; detritus, 15; Cocconeis, 25; Epithemia, 20; diatoms, 5. Gregarina.
5589b	3. Brachycentrus....	Aug. 26	Lamar River...	Minor rapids. Decaying Cladophora.	Melosira, 10; mayfly fragments, 20; Chironomus, 5; Trebonema, 20; Cocconeis, 30; Epithemia, 10; diatoms, 5; Gregarina.
5589b	4. Brachycentrus....	Aug. 26	Lamar River...	Minor rapids. Decaying Cladophora.	Melosira, 5; detritus, 20; Cocconeis, 30; Epithemia, 40; diatoms, 5. Gregarina.
5589b	5. Brachycentrus....	Aug. 26	Lamar River...	Minor rapids. Decaying Cladophora.	Melosira, 5; Cocconeis, 20; Epithemia, 65; diatoms, 10. Gregarina.
5589b	6. Brachycentrus....	Aug. 26	Lamar River...	Minor rapids. Decaying Cladophora.	Ameletus fragments, 40; Chironomus pupae, 5; Cocconeis, 10; Epithemia, 40; diatoms, 5. Gregarina.

Table No. 5.—Showing Food of Trichoptera.—(*Continued*).

Collection Number	Specimen Number and Name	Date, 1921	Locality	Habitat	Food in Percentages
5589b	7. Thremma	Aug. 26	Lamar River	Minor rapids. Decaying Cladophora.	Epithemia, 100.
5590a	12. Rhyacophila	Aug. 26	Yellowstone R.	Moderate rapids	Cladophora, 5; detritus, 95.
5590b	5. Rhyacophila	Aug. 26	Yellowstone R.	Rapids along shore	Ephemerella fragments, 40; Chironomus, 40; Trebonema, 5; detritus, 15.
5590b	6. Rhyacophila	Aug. 26	Yellowstone R.	Rapids along shore	Wood fragments, 50; Trebonema, 5; detritus, 45.
5590b	7. Rhyacophila	Aug. 26	Yellowstone R.	Rapids along shore	Insect fragments, 15; detritus, 85.
5590b	8. Rhyacophila	Aug. 26	Yellowstone R.	Rapids along shore	Trebonema, 10; detritus, 90.
5590b	9. Rhyacophila	Aug. 26	Yellowstone R.	Rapids along shore	Detritus, 50; Trebonema, 20; Cladophora, 5; moss leaves, 15; wood fragments, 10.
5590b	10. Rhyacophila	Aug. 26	Yellowstone R.	Rapids along shore	Chironomus, 20; detritus, 80.
5590b	11. Rhyacophila	Aug. 26	Yellowstone R..	Rapids along shore	Insect fragments, 90 Chironomus, 10.
5591a	1. Hydropsyche	Aug. 27	Tower Creek	Minor rapids	Insect fragments, 100.
5591a	2. Rhyacophila	Aug. 27	Tower Creek	Minor rapids	Unrecognizable matter (detritus?), 100. Gregarina.
5591a	3. Rhyacophila	Aug. 27	Tower Creek	Minor rapids	Insect fragments, 80; detritus, 20. Gregarina.
5591a	4, 5. Rhyacophila	Aug. 27	Tower Creek	Minor rapids	Detritus, 100. Gregarina.
5591a	6. Thremma	Aug. 27	Tower Creek	Minor rapids	Detritus, 100. Gregarina.
5591a	7. Thremma	Aug. 27	Tower Creek	Minor rapids	Detritus, 100. Gregarina.
5591a	30. Rhyacophila	Aug. 27	Tower Creek	Minor rapids	Insect fragments, 100.
5591b	1. Hydropsyche	Aug. 27	Tower Creek	Strong rapids	Mayfly fragments, 98; Chironomus, 2.
5591b	2. Rhyacophila	Aug. 27	Tower Creek	Strong rapids	Detritus, 100. Few Gregarina.
5591b	3. Rhyacophila	Aug. 27	Tower Creek	Strong rapids	Insect fragments, 100. Few Gregarina.
5591b	4. Thremma	Aug. 27	Tower Creek	Strong rapids	Diatoms, 1; detritus, 99.
5591b	5. Thremma	Aug. 27	Tower Creek	Strong rapids	Diatoms, 5; detritus, 95.
5591c	1. Rhyacophila	Aug. 27	Tower Creek	Lateral pool, with moderate current.	Detritus, 100.

Table No. 6.—Showing Summary of Food of Trichoptera.

Name	Locality	Number of Specimens		Animal Food	Plant Food	Detritus
Rhyacophila	Yellowstone River	8		27	16	57
Rhyacophila	Lost Creek	14		57	43	....
Rhyacophila	Tower Creek	10		55	....	45
Average for		32	=	49	23	28
Hydropsyche	Yellowstone River	3		48	20	32
Hydropsyche	Lost Creek	22		35	64	....
Hydropsyche	Tower Creek	2		100	....	....
Average for		27	=	42	54.3	3.7
Brachycentrus	Yellowstone River	1		....	65	35
Brachycentrus	Lamar River	32		19	73	8
Average for		33	=	18.3	72.7	9
Thremma	Yellowstone River	1		....	55	45
Thremma	Lamar River	5		....	100	....
Thremma	Lost Creek	11		....	80	20
Thremma	Tower Creek	6		....	2	98
Average for		23	=		64	36

Of the results obtained from the study of the stomach contents of insects, those from trichopterous stomachs are perhaps of most interest. Of these results the following might be said: (1) Each species must be judged by itself. Some species seem to have a large percentage of animal matter in their diet, others little or none at all. (2) Those feeding on animal matter are inclined to be cannibalistic. (3) Local conditions beget local results. A species may have a large animal diet in one locality, and a large plant diet in a different locality. (4) About sixty per cent of the caddisworms are parasitized by gregarines. It was thought possible to establish a correlation between the number parasitized and the amount of animal food taken. Thus, *Rhyacophila* with an animal diet of 49% was parasitized to about 45%, and *Hydropsyche* with an animal diet of 42%, to 60%. In contrast to this, *Brachycentrus* with the much smaller percentage of 18.3 animal matter was parasitized practically 100%. Hence no correlation can be said to exist.

The findings of other writers seem to corroborate the foregoing conclusions, especially 1, 2, and 3. Thus Muttkowski ('18, p. 442) calls attention to the fact that caddisworms readily exchange a phytophagous for a sarcophagous diet. Felber ('08) remarks on the avidity of *Halesus* larvae. These are carnivores, and not only do they not content themselves with smaller animals as food, but may even attack larger animals. Thus on one occasion Felber noted that some fifteen larvae clung to a Triton in an aquarium. Next day the salamander was dead and the skeleton had been practically stripped.

Lloyd ('21) in a series of detailed studies of various caddisflies brings together considerable data as to the food of the larvae. In successive order the food is noted for the following species:

Neuronia postica, stygipes, and *pardalis*—leaves in all stages of preservation.

Phryganea interrupta, and *vestita*—green plant tissues in natural environment, in the laboratory any plant food.

Limnophilus combinatus—vegetable matter, some diatoms.

L. indivisus—vegetable matter, without discrimination, decaying tissues in greater abundance.

D. submonilifer—raspings from sticks and plants, diatoms and other microscopic organisms, as well as wood or plant fragments.

Arctoecia consicia—shallow raspings from sticks and vegetation.

Astenophylax argus—dead bark and wood.

Pycnopsyche scabripennis—raspings of decomposed wood.

Platyphylax designata—young larvae with diatoms; large larvae with diatoms, sand, and fragments of higher plants. Vorhies lists "watercress and watermilfoil."

Halesus guttifer—fine raspings of decomposed wood.

Chilostigma difficilis—fragments of wood and leaves.

Brachycentrus nigrisoma—diatoms at first, then green algae and seed plants; carnivorous at the end of six weeks.

Mystacides sepulchralis—masticated pulp of vegetable origin.

Hydropsychidae—young larvae on green and blue-green algae. Older larvae tend to be carnivores.

Polycentropus—plankton and small insects.

Rhyacophilidae—filamentous algae and small larvae.

The last three are the types noted for their animal food in Yellowstone Park. It would seem, therefore, that the animal diet of these species is not confined to inhabitants of trout streams of the West.

The Food of Diptera. The following table gives in detail the food percentages of the specimens studied.

TABLE No. 7.—SHOWING THE FOOD OF DIPTERA.

Collection Number	Specimen Number and Name	Date, 1921	Locality	Habitat	Food Material Percentages
5566b	2. Chironomus sp...	Aug. 10	Lost Creek....	From Melosira..........	Melosira, 50; Cymbella, 50.
5566j	4. Chironomus sp...	Aug. 10	Lost Creek....	From barrens with a few diatom shells.	Sand, 80; diatoms, 20.
5566k	3. Chironomus sp...	Aug. 10	Lost Creek....	From barrens with a few diatom shells. Some Closterium.	Diatoms, 5; sand, 95.
5566l	6. Chironomus sp...	Aug. 10	Lost Creek....	Nearly pure Oscillatoria with a trace of Melosira.	Oscillatoria, 95; diatoms, 5.
5567a	13. Tipulid larva.....	Aug. 11	Yellowstone R.	Rapids.................	Juices of other animals?, 100.
5567a	14. Tipulid larva.....	Aug. 11	Yellowstone R.	Rapids.................	Juices of other animals?, 100.
5567a	37. Tanytarsus larva.	Aug. 11	Yellowstone R.	Rapids.................	Diatoms, 95; sand, 5.
5567a	38. Tanytarsus larva.	Aug. 11	Yellowstone R..	Rapids.................	Diatoms, 100.
5567a	41. Simulium sp.....	Aug. 11	Yellowstone R.	Rapids.................	Shore diatoms, 45; Rhizoclonium, 5; lake plankton, 50.
5567a	42, 43, 44, 45. Simulium sp.	Aug. 11	Yellowstone R.	Rapids.................	Shore diatoms, 45; Rhizoclonium, 5; lake plankton, 50.
5567a	46. Simulium sp.....	Aug. 11	Yellowstone R.	Rapids.................	Shore diatoms, 80; lake plankton, 20.
5567a	47. Simulium sp.....	Aug. 11	Yellowstone R.	Rapids.................	Shore diatoms, 80; lake plankton, 20.
5589a	22. Simulium sp.....	Aug. 26	Lamar River...	Strong rapids on moss and Cladophora.	Trebonema, 1; diatoms, 60; Cladophora, 1; detritus, 38.
5590c	12. Simulium sp.....	Aug. 26	Yellowstone R.	Strong rapids. Violent current.	Detritus, 50; diatoms, 45; green algae, 5.
5590c	13, 14, 15. Simulium sp.	Aug. 26	Yellowstone R.	Strong rapids. Violent current.	Detritus, 50; diatoms, 45; green algae, 5.
5590c	16. Simulium sp.....	Aug. 26	Yellowstone R.	Strong rapids. Violent current	Detritus, 50; diatoms, 45; green algae, 5. Parasitized by Mermis (?).
5590c	17. Simulium sp.....	Aug. 26	Yellowstone R..	Strong rapids. Violent current.	Detritus, 50; diatoms, 45; green algae, 5. Parasitized by Mermis (?).

TABLE No. 8—SHOWING SUMMARY OF FOOD OF DIPTERA.

Name	Locality	Number of Specimens	Plant Food	Detritus
Chironomids............	Lost Creek.............	4	58	42
Chironomids............	Yellowstone River.......	2	97	3
Average for............		6	= 71	29
Simulium...............	Lamar River............	1	62	38
Simulium...............	Yellowstone River.......	14	80	20
Average for............		15	= 79	21

Probably more than three times the number of specimens listed of both chironomids and *Simulium* were examined, but since the contents were very much alike, it was not considered worthwhile to record them separately. What is noted here for the food of chironomids agrees in the main with prior data recorded by the senior author (Muttkowski, '18, p. 411) for species from Lake Mendota. The diet comprises primarily the micro-food so abundant in the slimy deposits on rocks.

For *Simulium* taken from Yellowstone River the large percentage of lake plankton is of interest. The source of this is Yellowstone Lake, some forty miles above the point where the *Simulium* were taken. A check made with catches from a fine plankton net showed a somewhat similar proportion of lake plankton and river algae and diatoms.

A considerable number of the *Simulium* were parasitized by a nematode (*Mermis?*). In the field notes of the senior author, under date of Aug. 15, 1921, Yellowstone River, the following remarks are relevant: "*Simulium* taken with *Mermis* (?) emerging. Young *Pteronarcys* nymphs (black at this stage) found feeding among the larvae and pupae. Enemies feeding on *Simulium* are fish and Perlids, and perhaps mayflies. Parasites were found in about one third of the larvae." Another note, dated Aug. 11, is as follows: "All swollen individuals (of *Simulium*) were parasitized. It was not determined whether any pupae were parasitized or if parasitized individuals could pupate. It was evident that the *Mermis* were leaving the larvae for their adult free-living stage. Just at what point they left the *Simulium* larvae was not determined. It was noted, however, that the parasite was coiled chiefly at the posterior end of the larva, with a small coil near the head."

Comparative Summary of the Food of Insects. Even from so brief a study as the foregoing certain facts can be gleaned. The most notable point is that aquatic insects in rapid streams are opportunists as regards food and eat whatever becomes available. Secondary to this is the fact that the aquatic insects forage extensively, and migrate freely in search of food.

Both of these points become evident from the collections made in Lost Creek, where special efforts were made to select various spots in the creek for sample collections of food and of specimens in the vicinity or upon that food. Reference to the stomach contents of the individual specimens and comparison with the food items listed for the particular spot shows at once that the large majority of specimens contained food that did not occur within many feet of the particular locality. This indicates that these species must be rovers and foragers to a marked extent, and that they are opportunists on the whole and eat whatever is available.

Environmental conditions in mountain streams are strenuous; the strong current in particular makes life somewhat precarious and selective feeding difficult. Hence as a result the diet becomes diversified; the insects take whatever comes along, be it plant, detritus, or animal matter. Their diet thus becomes much more generalized than the diet of related species in more permissive habitats, such as ponds and slow streams. In the latter the less strenu-

ous conditions permit the insects to select their food, that is, to restrict their diet to favored food, and to search for that food.

In other words, specialization of habitat leads to diversification of diet, while generalization of habitat permits a restriction of diet.

The following table gives a comparative summary of the food of the insects studied.

TABLE NO. 9.—SHOWING COMPARATIVE SUMMARY OF FOOD OF INSECTS. (EMPTY STOMACHS NOT INCLUDED IN THE COMPUTATIONS).

	Name	Number of Specimens		Animal Food	Plant Food	Detritus
Perloidea	Pteronarcys	26		3.85	53.85	42.3
Perloidea	Acroneuria	49		77.4	6.3	16.3
Perloidea	Perla	5		85	15	....
Average for		80	=	54	22.3	23.7
Ephemeroidea	Ameletus sp	25		....	22.7	77.3
Ephemeroidea	Baetis sp	2		....	50	50
Ephemeroidea	Drunella sp	20		18.5	36.8	44.7
Ephemeroidea	Ephemerella sp	28		3.7	36.3	60
Ephemeroidea	Heptagenia sp	34		....	24	76
Average for		109	=	4.3	29.7	66
Trichoptera	Rhyacophila	32		49	23	28
Trichoptera	Hydropsyche	27		42	54.3	3.7
Trichoptera	Brachycentrus	33		18.3	72.7	9
Trichoptera	Thremma	23		....	64	36
Average for		115	=	28	54	18
Diptera	Chironomidae	6		....	71	29
Diptera	Simulium	14		....	79	21
Average for		20			76.6	23.4

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References to food of aquatic insects are exceedingly scant. As a rule they consist of brief notations in papers devoted to the biology and metamorphosis of aquatic forms.

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